REVIEW

DIVERSITY AND ADAPTATIONS OF RHEOPHYTIC FERNS

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ABSTRACT

Rheophytes grow in the zone on river beds and banks that are regularly flooded after heavy rains. In the tropics, this zone is of sufficient height (from the lowest to the highest water level) that different rheophytes can occur in the lower and upper subzones. Rheophytic species are obligate or facultative and some woody plants, rarely climbers, are paedorheophytic. I enumerate 141 rheophytes and possible rheophytes in 18 families and subfamilies of rheophytic ferns and lycophytes assigned to a variety of families, suggesting recurrent adaptations. The rheophyte morphology is adapted to the habitat and shared among the lineages, and especially the leaves or leaflets are streamlined with cuneate bases and glabrous, entire, tough blades. In leaf development the mesophyll cells and intercellular spaces, together with the epidermal cells, are smaller in size during a shortened period of ontogeny. The gametophyte of rheophytes, which is independent of the sporophyte, has a different adaptive strategy from the sporophyte: a shortened duration of generation and subtle morphological modification.

ECOLOGY

Plants include 300,000–330,000 or more species of bryophytes, lycophytes, ferns, gymnosperms and angiosperms (Evert and Eichhon, 2013; Mauseth, 2014). They grow in a wide range of habitats other than terrestrial, including alpine, arid, water, mangrove swamp, epiphytic, lithophytic (e.g., on limestone or ultramafic rocks), and other habitats (Crawford, 2008). The habitats are characterized by abiotic factors (temperature, precipitation, light, etc.) and associated organisms. Remarkable organismal associations are seen in, for example, symbiotic plants (Paracer and Ahmadjian, 2000; Evert and Eichhorn, 2013). This paper reviews our understanding of the diversity and adaptations of ferns that grow in rivers.

A special habitat for plants is provided by rivers. Rivers are often subject to flash floods after heavy rains, even as frequently as once a week in the tropics, and plants called rheophytes grow exclusively on banks and beds of rivers and streams (van Steenis, 1981, 1987; Mehtreter, 2008). Van Steenis (1981) defined rheophytes in ecological terms as follows: rheophytes are "confined to the bank and bed and growing there up to flood level, but not beyond the reach of regularly occurring flash floods" (Figure 1). Rheophytes are largely tropical, but a few extend into temperate zones, e.g., Hokkaido, in northern Japan (43°N) (Iwatsuki, 1992). Most rheophytes live in the air much longer than under relatively brief flooded conditions; this is because water levels return to the

more normal levels shortly after rains stop or abate. A few other rheophytes are hydrophytic and always grow submerged, as in e.g., *Hymenasplenium obliquissimum* (Hayata) Sugim. & Sa. Kurata.

Similar habitats are present in seasonally inundated pools, where semiaquatic ferns, such as *Platyzoma microphylla* R.Br. (=*Pteris platyzomopsis* Christenh. & H.Schneid.) (Tryon, 1964) and *Marsilea* species (Kornas, 1988) grow, and in inundated riparian and marshland forests, which are one of the habitats preferred by, e.g., *Osmunda regalis* L. (Lellinger, 1985; Page, 1997). However, the lands are covered by still or slow-running water.

The height of the flood zone, from the normal low level of river water to the highest flood level reached, differs in different climates -- up to 3 metres in humid tropical Borneo (Figure 1; M. Kato, unpubl. data). There are different preferences of rheophytes for the tropical flood zone. Some rheophytes, e.g., *Ctenitis vilis* (Kunze) Ching, grow in the higher zone, which is subject to rarer and shorter floods, while others, e.g., *Microsorum pteropus* (Blume) Copel., prefer the lower zone, which is subject to more frequent and longer floods. *Microsorum paucijugum* (Alderw.) K.Iwats. & M.Kato prefers the further lower zone.

Rheophytes are herbaceous or woody. In herbaceous rheophytes, whole plants are submerged when flooded, while in tall woody rheophytes only the basal part of the plant is submerged while flooded. In tall paedorheophytes, seedlings and low juveniles are rheophytic and the adults are emergent and thus typically not rheophytic. *Alsophila esmeraldensis* R.C.Moran of the tree-fern family Cyatheaceae is regarded as a rheophyte (Moran, 1995), but it may not be paedorheophytic because of the short (up to 80 cm) trunk. Van Steenis (1987) considered *Lomagramma* species as paedorheophytic, because

Figure 1. Habitat segregation of rheophytes and land species on river bank in West Kalimantan, Indonesia. Rheophytic *Dipteris lobbiana* occupies the flood zone, and land species such as *D. conjugata* Reinw. and *Blechnum orientale* L. grow above the zone

the juvenile creeping plants are rheophytic and only later climb trees. Further study is necessary to reveal paedorheophily of ferns.

Rheophytes may be obligate or facultative. Usually, obligate-rheophytic species comprise only rheophytic populations, while facultative rheophytes comprise land-dwelling populations and rheophytic populations. Examples of facultative rheophytic ferns are *Bolbitis heteroclita* (C.Presl) Ching in C.Chr. and *B. sinuata* (C.Presl) Hennipman. *Ampelopteris prolifera* (Retz.) Copel. and *Diplazium esculentum* (Retz.) Sw. may also belong to this category.

ADAPTIVE MORPHOLOGY

The impact of flash floods to plants is considerable because non-rheophytic land plants cannot invade the flood zone (Figure 1). Rheophytes have gained particular morphologies to resist or reduce pressure of flooding, although their leaves may be damaged by flooding (Sharpe, 1997). The shoot-branches and leaf-petioles are flexible or tough with developed bark in, e.g., *Salix* or with dense networks of cell walls in *Osmunda* (Imaichi and Kato, 1992). The roots adhere tightly to the river bank and bed. The most remarkable feature of rheophytes is leaf morphology (van Steenis, 1981). The leaves or leaflets are streamlined (usually narrow-lanceolate) with cuneate bases (Figure 2), entire or only minutely toothed at the margins, and hairless or sparsely hairy. Cuneate leaf-bases are particularly important because the bases are under pressure from currents. Thelypteridaceae, a large family generally characterized by having hairy leaves, has the largest number of rheophytes in ferns (Appendix), but the hairs of rheophytic species in this family are usually sparse, short, or antrorse (ascending or appressed toward the distal end of the lamina or pinnae). In paedorheophytes, only the leaves of juvenile plants are streamlined.

Sharpe (1997) found that in the Puerto Rican rheophyte *Meniscium angustifolium* Willd. the leaf growth rate is faster than in other tropical land ferns, and the leaf life-span is shorter. The faster growth rate would reduce exposure of the fragile uncoiling leaves

Figure 2. Pinnules. A. Land-living *Osmunda japonica*. B. Rheophytic *O. lancea*.

to flood, and the shorter life span would allow escape from stresses of flooding. The leaf phenology of rheophytic ferns should be further investigated to clarify the various adaptations (see also section "Adaptations").

DIVERSITY

Rheophytic ferns are most abundant in tropical areas with heavy rainfall, and van Steenis (1981, 1987) enumerated 67 rheophytic ferns and lycophytes. Kato et al. (1991) found about 40 species of rheophytic ferns from Borneo. It indicates that the ever-wet Borneo is remarkably species-rich for rheophytes. At present 141 rheophytic fern taxa are known in the world, and these are assigned to 18 families and subfamilies (Appendix 1). There are other species that require further study with respect to whether they are rheophytic or not.

In many fern genera, only one or a few rheophytic species are known, while there are multiple rheophytes in other genera. This trend is obvious also in flowering-plant rheophytes, believed to be about 800 (0.3% of the total number) species belonging to 68 (17%) families (van Steenis, 1981, 1987). The scattered distribution of rheophytes over many lineages suggests that derivation of rheophytes from land-growing ancestors is markedly recurrent. Some rheophytes are secondarily derived from other rheophytic species in the same genus. I suggest that *Microsorum paucijugum* (Alderw.) K.Iwats. & M.Kato growing in the lower flood zone is derived from another rheophytic *M. pteropus*. Kato (1984) considered that two rheophytes, *Deparia biserialis* (Baker) M.Kato and *D. confluens* (Kunze) M.Kato, are derived from *D. petersenii* (Kunze) M.Kato, although molecular evidence to support these relationships is not available (Kuo et al., 2016). Rheophytic fern species are distributed in a wide range of ferns (PPG I, 2016) from the primitive Osmundaceae through the derived Polypodiaceae, and even in the eusporangiate Ophioglossaceae and the lycophytic family Isoëtaceae. Most fern families with rheophytic members are large (> 200 spp.) and tropical (for example, Thelypteridaceae). The most species-rich genus is *Bolbitis* (14 spp.), which prefers rock surfaces in wet valleys. I suggest that the evolution of rheophytes happened by chance in the tropics where the rheophytic habitats are abundant. However, the basal leptosporangiate families Osmundaceae and Dipteridaceae are small and comprise fewer than 20 species.

ADAPTATIONS

Narrow streamlined leaves are characteristic of rheophytes (van Steenis, 1981; Vasco et al., 2013). Kato and Imaichi (1992a) examined 32 tropical rheophytic ferns and related land species, and found a strong correlation between leaf morphology and anatomy. The mesophyll cells and intercellular spaces are smaller in the narrow leaves than in the broad leaves of related species. Correlated with this, the epidermal cells are also smaller (Kato and Imaichi 1992a). In a comparative developmental study, Imaichi and Kato (1992, 1997) showed that the mesophyll cells at the pre-expansion stage are cubical and equal-sized and then expand in both *Osmunda japonica* Thunb. and *O. lancea* Thunb. (Figure 3A, E). However, the expansion time-span is less and the mesophyll cell arms are shorter, surrounding the smaller intercellular spaces, in *O. lancea* (Figure 3). In this study, we interpreted the evolution of the narrow leaves as heterochronic. Kato and Imaichi (1992b) found a broad-leaved variant of the rheophytic *Tectaria lobbii* (Hook.) Copel.in East Kalimantan. This variant grew together with the normal form and differed only in the broad pinnae with irregular lobes (Figure 4A, C). The broad-leaved variant

may have been called *T. jacobii* Holttum (Holttum, 1991). It is anatomically very similar to land-growing species (Figure 4B, D), suggesting atavism.

Cells of petioles of the rheophytic *Osmunda lancea*, like those of the lamina, are smaller and denser, the cuticular layer is thicker, and the epicuticular wax deposits are denser than in *O. japonica* (Imaichi and Kato, 1992, 1993). This leaf construction increases mechanical strength and repels water (Juniper and Walker, 1985). Exceptional flooding (to a height of 10 metres above the normal level of water) rarely reached terrestrial ferns growing well above the flood zone and if this happens, it may decay their leaves (M. Kato, unpublished field observations). This contrasts with rheophytes, which have high resistance to regular flooding in fast-moving, sometimes violent, currents containing dense microbes and soil/rock particles.

There is a clear habitat separation between rheophytes and land plants at the uppermost reaches of flood zones (Figure 1). Land-growing species cannot invade the flood zone, due to their non-adaptive morphology. It is likely that the habitat separation is established in a certain stage of life cycle. Imaichi and Kato (1993) showed that juvenile plants of *Osmunda japonica* grow together with the rheophytic *O. lancea* near the water, and morphological and anatomical differences become prominent at an early ontogenic stage (plants having 5th or 6th youngest leaves). We suggested that *O. japonica*

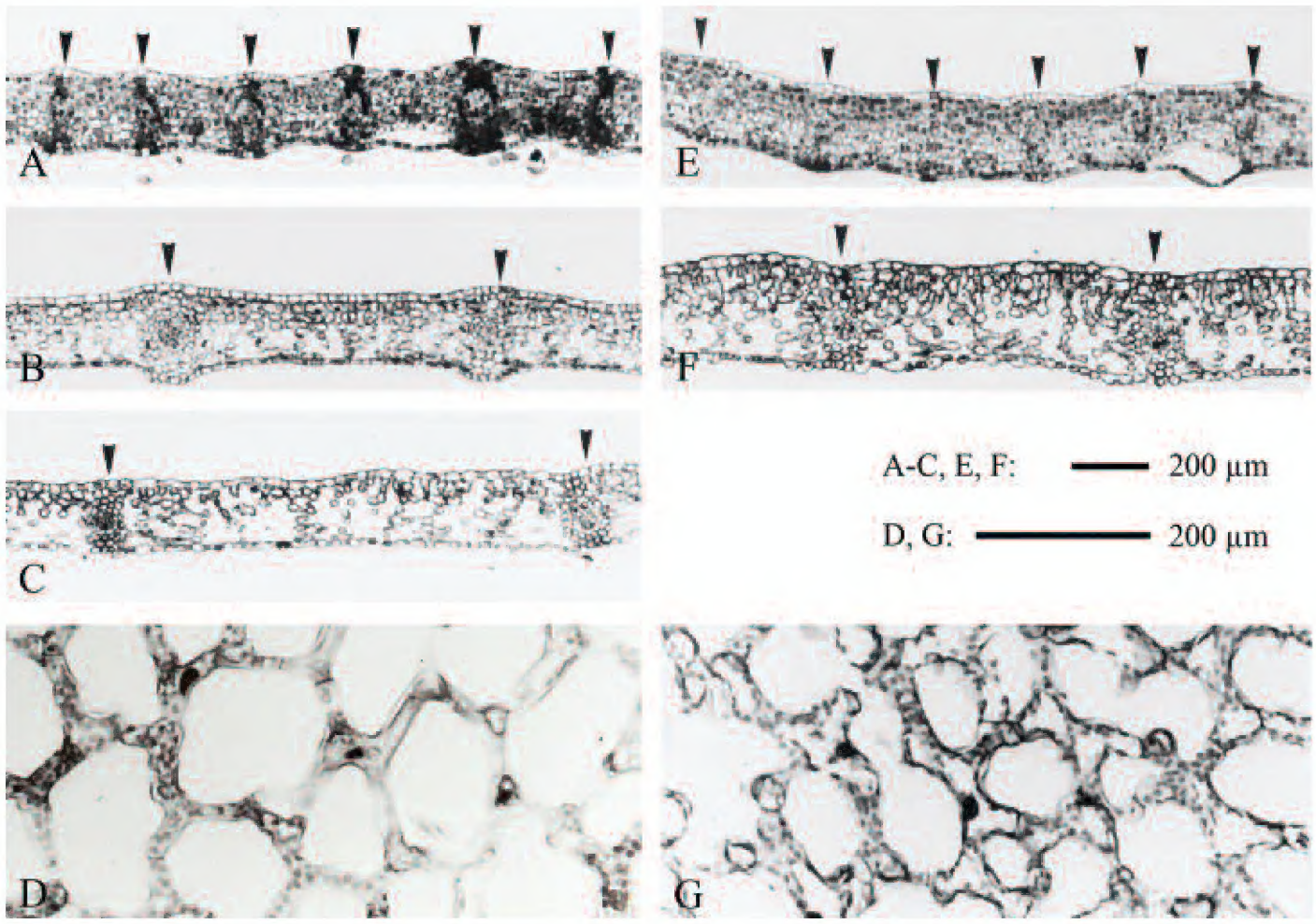

Figure 3. Cross sections of pinnules at different stages of development (A–C, E, F) and paradermal sections of mature pinnules (D, G). A–D. *Osmunda japonica*. A, B. Young pinnules (A, 12 mm long; B, 43 mm). C. Mature pinnule (71 mm). E–G. *O. lancea*. E. Young pinnule (12 mm). F. Mature pinnule (45 mm). Arrowheads indicate veins. *Osmunda japonica* in young stage (A) has as many unexpanded mesophyll cells between veins as has *O. lancea* (E) (Imaichi and Kato, 1992). The mature stage of *O. lancea* (F) is similar to an immature stage of *O. japonica* (B). Intercellular spaces are surrounded by armed mesophyll cells (D, G).

was selected and excluded early from the flood zone and the two species eventually become separated in space and habitat.

In contrast, *O. lancea* cannot extend its habitat above the flood zone. This restriction may be caused by the narrowed leaf area and reduced intercellular space in the mesophyll layer, which may reduce photosynthetic power. This anatomical and the suggested physiological character may be a trade-off. A reduced photosynthetic rate was found in the rheophyte *Farfugium japonicum* var. *luchuense* (Masam.) Kitam. (Asteraceae) (Nomura et al., 2006), although it has a different mesophyll anatomy from fern rheophytes (see below). The isolation of the flood zone from the land zone appears strong, but this is not always strong. The diploid hybrid of *O. japonica* and *O. lancea* [= *O.* ×*intermedia* (Honda) Sugimoto] occurs in the interface between both habitats and can reproduce F2 or later offspring (Yatabe-Kakugawa et al., 2013).

Ferns and lycophytes are characterized by the independence of the sporophyte and gametophyte. It is likely that the two generations have different adaptive strategies. The gametophyte generation is much smaller, simpler, and shorter-lived. There is little morphological difference between gametophytes of *O. japonica* and *O. lancea* (Hiyama et al., 1992). Hiyama et al. (1992) discovered that in the rheophytic *O. lancea* the life span of gametophytes is shorter and they interpreted that its gametophyte generation is shortened, relative to land ferns, showing a different strategy from the sporophyte.

Compared with the ferns investigated, the leaves of flowering plant rheophytes show different anatomy. Narrow leaves of the facultative-rheophyte *Farfugium japonicum* var.

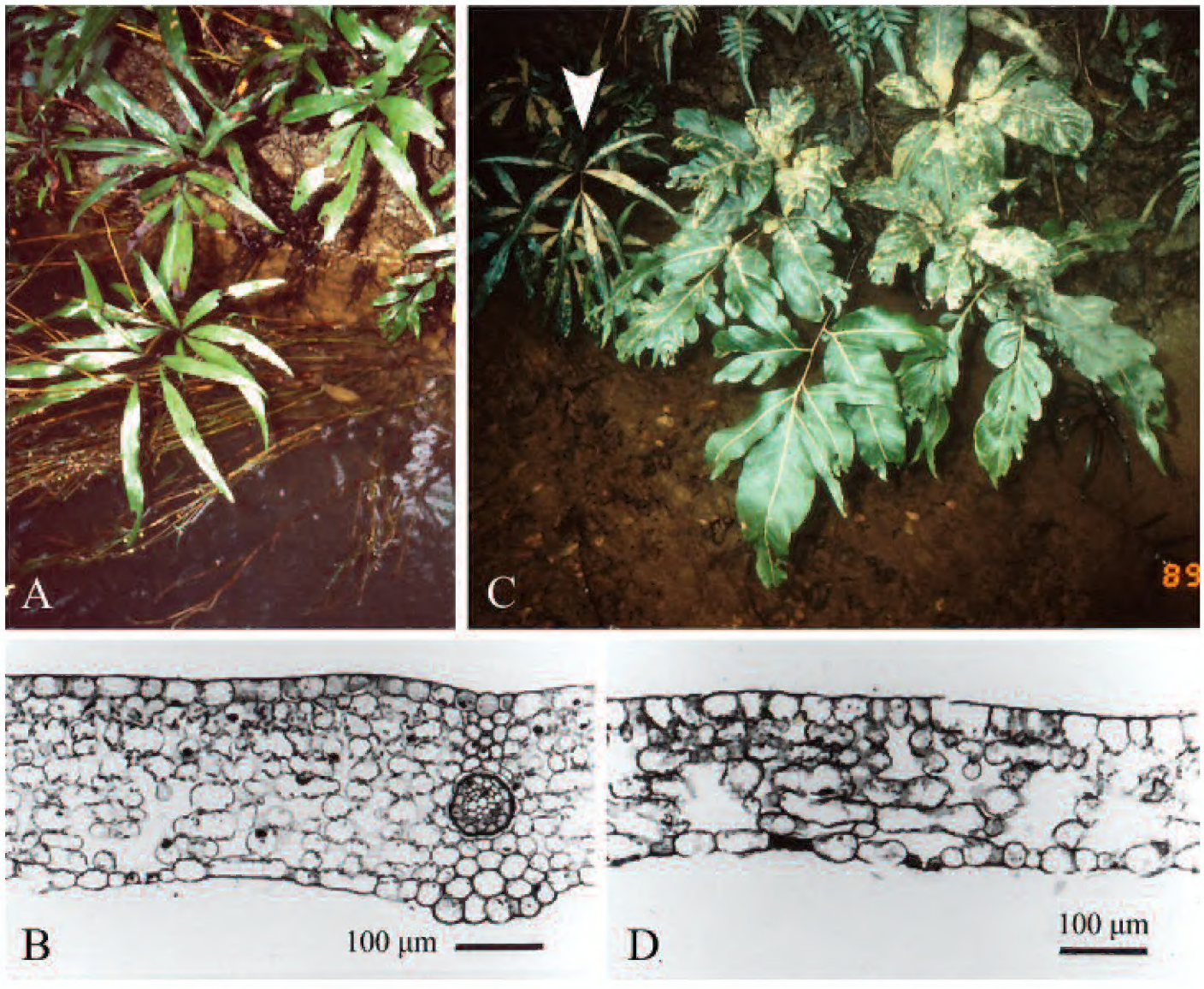

Figure 4. Rheophytic *Tectaria lobbii*. A, B. Normal plants. C, D. Broad-leaved plants. In C, arrowhead indicates normal plants. B, D. Cross sections of pinnules.

luchuense have fewer mesophyll cells than the broad-leaved form (Usukura et al., 1994). Similar anatomy was found in other flowering plant rheophytes (Tsukaya, 2002; Setoguchi and Kajimaru, 2004; Okada and Tsukaya, 2010, 2013; Vermeulen and Tsukaya, 2011; Ohga et al., 2012; Matsui et al., 2013). However, a rheophytic orchid ecotype shows fern-type anatomy (Yorifuji et al., 2015).

EVOLUTION

The pattern in which rheophytic ferns are scattered in various genera and families indicates that similar modes of adaptations produced rheophytes in a number of independent lineages (Kato et al., 1991). However, the phylogenetic relationships of rheophytic ferns have been clarified in only a few cases (e.g., *Osmunda*, Tsutsumi et al., 2012; *Deparia*, Kuo et al., 2016). Most rheophytes are obligate-rheophytic species, while some others are distinguished at varietal rank, e.g., *Deparia lancea* var. *rheophila* M.Kato, Darnaedi & K.Iwats., *Lindsaea ensifolia* var. *rheophila* K.Iwats. Still others, e.g., *Bolbitis heteroclita* and *B. sinuata* (C.Presl) Hennipman, are facultative and grow in both habitats. Little is known about the evolutionary process of rheophytes. One question to solve is whether facultative rheophytes or rheophytic varieties are transitional toward obligate rheophytes. Another is whether speciation of rheophytes is gradual or abrupt.

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APPENDIX

Rheophytic ferns and suggested rheophytes. Family or subfamily names are followed by numbers of taxa.

Aspleniaceae (9) --- *Asplenium delicatulum* C.Presl, *Asplenium dichotomum* Hook. [facultative], *Asplenium subaquatile* Ces., *Asplenium triculum* A.R.Sm.; *Hymenasplenium murakami-hatanakae* Nakaike, *Hymenasplenium obliquissimum* (Hayata) Sugim. & Sa. Kurata, *Hymenasplenium obtusifolium* (L.) L.Regalado & Prada, *Hymenasplenium riparium* (Liebm.) L.Regalado & Prada [facultative], *Hymenasplenium triquetrum* (N. Murak. & R.C. Moran) L.Regalado & Prada

Athyriaceae (7) --- *Athyrium haleakalae* K.R.Wood & W.L.Wagner; *Deparia biserialis* (Baker) M.Kato, *Deparia confluens* (Kunze) M.Kato, *Deparia lancea* (Thunb.) Fraser-Jenk. var. *rheophila* (M.Kato, Darnaedi & K.Iwats.) M.Kato; *Diplazium aequibasale* (Baker) C.Chr., *Diplazium esculentum* (Retz.) Sw. [facultative], *Diplazium wahauense* M.Kato, Darnaedi & K.Iwats.

Blechnaceae (6) --- *Austroblechnum difforme* (Copel.) Gaspe & V.A.O.Dittrich; *Cranfillia fluviatilis* (R.Br.) Gaspe & V.A.O.Dittrich; *Oceaniopteris francii* (Rosenst.) Gaspe & Salino, *Oceaniopteris gibba* (Lab.) Gaspe & Salino; *Parablechnum glaziovii* (Christ) Gaspe & Salino, *Parablechnum rheophyticum* (R.C.Moran) Gaspe & Salino

Cyatheaceae (1) --- *Alsophila esmeraldensis* R.C.Moran

Dennstaedtiaceae (1) --- *Microlepia rheophila* K.Iwats. & M.Kato

Dipteridaceae (1) --- *Dipteris lobbiana* (Hook.) T.Moore

Dryopteridaceae subfamily Dryopteroideae (3) --- *Ctenitis vilis* (Kunze) Ching [facultative]; *Dryopteris rheophila* Mitsuta ex Darnaedi, M.Kato & K.Iwats.; *Polystichum yaeyamense* (Makino) Makino

Dryopteridaceae subfamily Elaphoglossoideae (17) --- *Bolbitis fluviatilis* (Hook.) Ching in C.Chr., *Bolbitis heteroclita* (C.Presl) Ching in C.Chr. [facultative], *Bolbitis heudelotii*

(Bory) Alston, *Bolbitis interlineata* (Copel.) Ching in C.Chr. [facultative], *Bolbitis interpreta* (C.Presl) Hennipman [rheophyte?], *Bolbitis presliana* (Fée) Ching in C.Chr., *Bolbitis quoyana* (Gaud.) Ching in C.Chr., *Bolbitis repanda* Schott, *Bolbitis rivularis* (Brack.) Ching in C.Chr., *Bolbitis salicina* (Hook.) Ching in C.Chr., *Bolbitis* ×*singaporensis* Holttum [rheophyte?], *Bolbitis sinuata* (C.Presl) Hennipman [facultative], *Bolbitis taylorii* (F.M.Bailey) Ching in C.Chr.; *Elaphoglossum dumrongii* Tagawa & K.Iwats., *Elaphoglossum resiniferum* Holttum, *Elaphoglossum rheophilum* M.Kato, Darnaedi & K.Iwats.; *Mickelia furcata* R.C.Moran, Labiak & Sundue

Hymenophyllaceae (2) --- *Cephalomanes javanicum* C.Presl var. *asplenioides* (C.Presl) K.Iwats. and var. *sumatranum* (Alderw.) K.Iwats. [facultative]

Isoëtaceae (2) --- *Isoëtes hawaiiensis* W.C.Taylor & W.H.Wagner [facultative], *Isoëtes martii* A.Br. ex Kuhn

Lindsaeaceae (13) --- *Lindsaea decaryana* (C.Chr.) K.U.Kramer [rheophyte?], *Lindsaea ensifolia* Sw. var. *rheophila* K.Iwats., *Lindsaea integra* Holttum, *Lindsaea lucida* Blume [facultative?], *Lindsaea plicata* Baker; *Odontosoria chinensis* (L.) J.Sm. var. *rheophila* (K.U.Kramer) Parris, *Odontosoria gracilis* (Tagawa) Ralf Knapp, *Odontosoria minutula* (Sa.Kurata) Ebihara; *Osmolindsaea odorata* (Roxb.) Lehtonen & Christenh. [facultative], *Osmolindsaea japonica* (Baker) Lehtonen & Christenh.; *Tapeinidium pinnatum* (Cav.) C.Chr. [facultative], *Tapeinidium prionoides* K.U.Kramer [facultative?]; *Xyropteris stortii* (Alderw.) K.U.Kramer

Ophioglossaceae (2) --- *Ophioglossum gramineum* Willd. var. *majus* (Alderw.) Wieferring, *Ophioglossum reticulatum* L. var. *dilatatum* (Miq.) Wieferring [facultative]

Osmundaceae (4) --- *Osmunda* (*Plenasium*) *angustifolia* Ching, *Osmunda* (*Plenasium*) *bromeliifolia* (C.Presl) Copel. [facultative?], *Osmunda hybrida* Tsutsumi et al. [rheophyte?], *Osmunda lancea* Thunb.

Polypodiaceae (14) --- *Calymmodon asiaticus* Copel.; *Leptochilus macrophyllus* (Blume) Noot. var. *fluviatilis* (Lauterb.) Noot., *Leptochilus minor* Fée [facultative?], *Leptochilus* ×*trifidus* Alderw.; *Loxogramme antrophyoides* (Baker) C.Chr. var. *rheophila* M.Kato, Darnaedi & K.Iwats.; *Microsorum krayanense* M.Kato, Darnaedi & K.Iwats.; *Microsorum paucijugum* (Alderw.) K.Iwats. & M.Kato, *Microsorum pteropus* (Blume) Copel., *Microsorum submarginale* M.Kato, Darnaedi & K.Iwats.; *Oreogrammitis universa* (Baker) Parris [facultative]; *Selliguea oodes* (Kunze) Hovenkamp, *Selliguea yakushimensis* (Makino) Fraser-Jenk.; *Xiphopterella alternidens* (Ces.) Parris; *Xiphopterella gracilis* Parris.

Pteridaceae subfamily Pteridoideae (2) --- *Pteris ensiformis* Burm.f. var. *rheophila* M.Kato, Darnaedi & K.Iwats.; *Taenitis interrupta* Hook. & Grev.

Pteridaceae subfamily Vittarioideae (3) --- *Antrophyum vittarioides* Baker [facultative?]; *Austrogramme asplenioides* (Holttum) Hennipman, *Austrogramme decipiens* (Mett.) Hennipman [facultative]

Tectariaceae (10) --- *Tectaria acutifolia* (Hieron.) Maxon, *Tectaria* ×*chaconiana* A.Rajas, *Tectaria fauriei* Tagawa [facultative?], *Tectaria jacobsii* Holttum, *Tectaria lobbii* (Hook.) Copel., *Tectaria menyanthidis* (C.Presl) Copel., *Tectaria microlepis* Holttum, *Tectaria rheophytica* Holttum, *Tectaria subdigitata* (Baker) Copel., *Tectaria trifida* (Fée) Price

Thelypteridaceae (44) --- *Amauropelta aspidioides* (Willd.) Pic.Serm., *Amauropelta consanguinea* (Fée) Salino & T.E.Almeida [facultative], *Amauropelta fluminalis* (A.R.Sm.) Salino & T.E.Almeida, *Amauropelta ptarmica* (Kunze ex Mett.) Pic.Serm., *Amauropelta rheophyta* (Proctor) Salino & T.E.Almeida, *Amauropelta sancta* (L.)

Pic.Serm., *Amauropelta saxicola* (Sw.) Salino & T.E.Almeida, *Amauropelta soridepressa* (Salino & V.A.O.Dittrich) Salino & T.E.Almeida, *Amauropelta villana* (L.D.Gómez) Salino & T.E.Almeida; *Ampelopteris prolifera* (Retz.) Copel. [facultative]; *Christella subpubescens* (Blume) Holttum [facultative]; *Goniopteris cumingiana* (Kunze) de Jonch. & S.Sen, *Goniopteris francoana* (E.Fourn.) A.Löve & D.Löve, *Goniopteris riograndensis* (Lindm.) Ching, *Goniopteris skinneri* (Hook.) Salino & T.E.Almeida; *Meniscium angustifolium* Willd., *Meniscium arborescens* Humb. & Bonpl. ex Willd. [facultative]; *Meniscium chrysodioides* Fée [facultative], *Meniscium lanceum* (A.R.Sm.) R.S. Fernandes & Salino [facultative], *Meniscium nesioticum* (Maxon & C.V.Morton) Pic.Serm. [facultative]; *Menisorus pauciflorus* (Hook.) Alston [facultative?]; *Mesophlebion oligodictyon* (Baker) Holttum; *Plesioneuron prenticei* (Carr.) Holttum; *Pronephrium aquatiloides* (Copel.) Holttum, *Pronephrium firmulum* (Baker) Holttum, *Pronephrium heterophyllum* (C.Presl) Holttum [rheophyte?], *Pronephrium hosei* (Baker) Holttum, *Pronephrium menisciicarpon* (Blume) Holttum, *Pronephrium peltatum* (Alderw.) Holttum var. *persetiferum* Holttum [rheophyte?], *Pronephrium rubidium* (Hook.) Holttum [rheophyte?], *Pronephrium salicifolium* (Wall. ex Hook.) Holttum; *Pseudocyclosorus falcilobus* (Hook.) Ching, *Pseudocyclosorus esquirolii* (Christ) Ching [facultative]; *Sphaerostephanos acrostichoides* (Desv.) Holttum (=*Thelypteris riparia* (Copel.) C.F.Reed), *Sphaerostephanos aquatilis* (Copel.) Holttum, *Sphaerostephanos cataractorum* (W.H.Wagner & Grether) Holttum, *Sphaerostephanos hispidifolius* (Alderw.) Holttum, *Sphaerostephanos mutabilis* (Brause) Holttum, *Sphaerostephanos perglanduliferus* (Alderw.) Holttum, *Sphaerostephanos warburgii* (Kuhn & Christ) B.C.Stone; *Steiropteris hottensis* (C.Chr.) Salino & T.E.Almeida, *Steiropteris wrightii* (Mett. ex D.C.Eaton) Pic.Serm.; *Trigonospora calcarata* (Blume) Holttum in B.K.Nayar & S.Kaur, *Trigonospora ciliata* (Benth.) Holttum

A SHORT BIOGRAPHY OF THE AUTHOR

Masahiro Kato was born in Japan in 1946. He graduated from Kyoto University and received Dr. Sci. in 1976 with a thesis entitled "Morphological and systematic studies of Athyriaceae." After being employed as research assistant in the Department of Botany, Kyoto University, he moved to the University of Tokyo in 1982 and became professor in 1997. Then he moved to the National Museum of Nature and Science as director of the Department of Botany and director of Tsukuba Botanical Garden. Now he is professor emeritus of the University of Tokyo and researcher emeritus of the National Museum of Nature and Science. He has undertaken a number of fieldwork projects over tropical Asia. His research interest has focused on the fern flora of tropical Asia, classification and systematics of pteridophytes, such as Athyriaceae, Davalliaceae, Ophioglossaceae and Osmundaceae. He has also investigated the evolution of epiphytic Davalliaceae, and explored rheophytes in Borneo and adjacent areas. In extended research of rheophytes, he has studied the flora, morphology and evolution of the torrenticolous rheophytes Podostemaceae (rosid angiosperms). This research extended into the genetic background of their unique morphology. Additionally, he researched the evolution of primitive angiosperms and single-leaf plants (*Monophyllaea*, Gesneriaceae), and the phylogenetic relationships of bryophytes and pteridophytes.

TWO HYBRIDS OF *EQUISETUM SYLVATICUM* (EQUISETACEAE) ON THE ISLAND OF SENJA, TROMS, NORWAY

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Key Words: *Equisetum sylvaticum*, hybrids, macromorphology, micromorphology, SEM, Senja, Norway, distribution

ABSTRACT

Equisetum ×mildeanum (*E. pratense* × *E. sylvaticum*) and *E. ×lofotense* (*E. arvense* × *E. sylvaticum*) have been discovered on the island of Senja (Troms, Norway). Their appearance in the field and macromorphology are extensively compared and imaged. Additionally micromorphological features of the shoot and stomata of both rare hybrid taxa and the involved parental species have been examined by SEM technology. Distribution maps illustrate the known occurrence for the European Nordic countries. A third taxon, *E. ×bowmanii* (*E. sylvaticum* × *E. telmateia*), is included in the comparative study to include all known *E. sylvaticum* hybrids in a single SEM investigation for the first time.

INTRODUCTION

Wood Horsetail, *Equisetum sylvaticum* L., belongs to the smooth horsetails (subgenus *Equisetum*) within the family of Equisetaceae (in comparison to the rough textured members of subgenus *Hippochaete* frequently called "scouring rushes") and is a delicate plant occurring over a wide range of wet woodland communities in the nemoral to boreo-arctic zone of Eurasia and North America (Hultén, 1950; Hultén & Fries, 1986; Jalas & Suominen, 1972).

Of the 11 hybrids that have been described within the subgenus (see overview in Lubienski, 2010; Page & Gureyeva, 2009; 2013) three have *E. sylvaticum* as one parent: *E. ×mildeanum* Rothm. (*E. pratense* Ehrh. × *E. sylvaticum*), *E. ×bowmanii* C.N. Page (*E. sylvaticum* × *E. telmateia* Ehrh.), and *E. ×lofotense* Lubienski (*E. arvense* L. × *E. sylvaticum*).

E. ×mildeanum was originally described from the Baltic Isle of Rügen of North Eastern Germany by Rothmaler (1944) and has been known to occur there since the 1950s (Lubienski, 2013; Lubienski & Dörken, 2015). More recently the hybrid has been recorded from Scotland (Page, 1988; Acock, 2015), Norway (Lubienski, 2003, 2009), and Sweden (Lubienski & Dörken, 2015). Unfortunately it is often confused with the parents, and its real distribution in the British Isles may be overestimated (see Acock, 2015).

E. ×bowmanii is recorded from a few localities within the New Forest area of Southern England (Page, 1988). Additionally a second site was reported from Scotland more recently (Acock, 2015), but this likely to be an error and confused with *E. sylvaticum* (H. McHaffie & P. Acock, pers. comm.). Consequently the New Forest sites remain exclusive for this unique plant.

In 2009 *E.* ×*lofotense*, a similarly remarkable hybrid incorporating *E. sylvaticum*, was detected at a single site in the far north of Norway on the Lofoten island of Austvågøya (Lubienski, 2010).

During a trip to the island of Senja (Troms, Norway) four colonies of *E. sylvaticum* hybrids were found. Two were identified as *E.* ×*mildeanum* and seem to fit into a series of *E.* ×*mildeanum* sites lying on the islands of North Western Norway, whereas the latter two represent the second record for *E.* ×*lofotense*. At first glance the two hybrid taxa are quite similar in habit and certain macromorphological features. Their adjacent sites allowed for study and direct comparison of their macromorphology *in situ*. Additional micromorphological investigation using SEM focused on the silica spikes on the ridges of the shoots and the structure of the stomata. As part of the morphological comparison, the hybrids were compared with *E. sylvaticum* and other taxa to confirm the identity of the second parents.

MATERIAL AND METHODS

Material

Plant material was collected on the the island of Senja (Troms province) that is located northeast of the Lofoten and Vesterålen islands. It is situated in the transition between the Northern and Middle boreal vegetation zone (Sjörs *et al.*, 2004). The islands and coastal mainland of Northwestern Norway display an oceanic climate with high precipitation values (Sjörs *et al.*, 2004).There are two colonies of each hybrid alongside a single fjord (Mefjorden) in the northern part of the island (Figure 1).

Figure 1. Mefjorden in the northern part of the island of Senja (Troms, Norway) showing the four sites of the *Equisetum sylvaticum* hybrids (*E.* ×*mildeanum* 1 & 2, *E.* ×*lofotense* 3 & 4) (based on Google Earth ©, Google Inc., 26.12.2016).

Equisetum ×*mildeanum* (*E. pratense* × *E. sylvaticum*)

1. Mefjorden near Svarthola, Berg kommune, Senja, Troms fylke
N 69°27'53.3" / E 17°34'29.2", c. 9 m a.s.l.

Growing over a length of approximately 90 metres along the wet western roadside ditch beneath the northeastern slope of Litlehesten mountain, south of Bratthesten tunnel (Figure 2a, b).

Figure 2. a, b. *Equisetum ×mildeanum* at its site near Svarthola (25.07.2016, M. Lubienski).

2. Mefjorden east of Mefjordvær, Berg kommune, Senja, Troms fylke
N 69°30'54.4" / E 17°28'08.2", c. 16 m a.s.l.

Occupying both ditches and shoulders of the road east of the town of Mefjordvær and west of Mykjeneset beneath the northern slope of Kyle mountain. The colony stretches over a length of approximately 100 metres (Figure 3a, b).

Figure 3. a, b. *Equisetum ×mildeanum* at its site near Mefjordvær (30.07.2016, M. Lubienski).

Equisetum ×lofotense (*E. arvense* × *E. sylvaticum*)

3. Mefjorden near Svarthola, Berg kommune, Senja, Troms fylke
N 69°27'42.2" / E 17°34'51.1", c. 5-13 m a.s.l.

Growing along a small creek that rises between the northeastern slopes of Store Hesten and Litlehesten mountain, crosses the road south of Bratthesten tunnel and flows into Mefjorden just a few metres beneath. The hybrid occupies the wet slope and the roadside ditch west of the road over an area of approximately 40 × 40 metres. The eastern side of the road descends to the sea and is colonized by *E. ×lofotense* over an area of approximately 40 × 5 metres (Figure 4a, b).

Figure 4. a, b. *Equisetum ×lofotense* at its site near Svarthola (25.07.2016, M. Lubienski).

4. Mefjorden north of Kvalvika, Berg kommune, Senja, Troms fylke
N 69°28'54.8" / E 17°33'15.9", c. 5-13 m a.s.l.

The site is situated by the same road two kilometres to the north, north of Bratthesten tunnel. The hybrid grows over an area 10 × 30 metres on the wet slope between Burstind and Bringtinden mountain and in the western roadside ditch; it is also found on the other (eastern) side of the road, where it accompanies a small rivulet to the sea (Figure 5 a, b).

Figure 5. a, b. *Equisetum ×lofotense* at its site near Kvalvika (25.07.2016, M. Lubienski).

Methods

Freshly collected shoots were fixed in FAA (100 ml FAA = 90 ml 70% ethanol + 5 ml acetic acid 100% + 5 ml formaldehyde solution 37%) before being stored in 70% ethanol. For SEM with AURIGA ZEISS TM the fixed material was dehydrated in FDA (formaldehyde-dimethyl-acetal) and critical-point dried (CPD 030, BALZERS). CP-dried material was sputtered with gold-palladium (thickness 5 nm) with a BALTEC SputterCoater SCD 030.

RESULTS

Comparison of morphology and field observations of *Equisetum ×mildeanum* and *E. ×lofotense* on Senja

In the field both hybrids appear similar to *E. sylvaticum* at first glance and look like odd

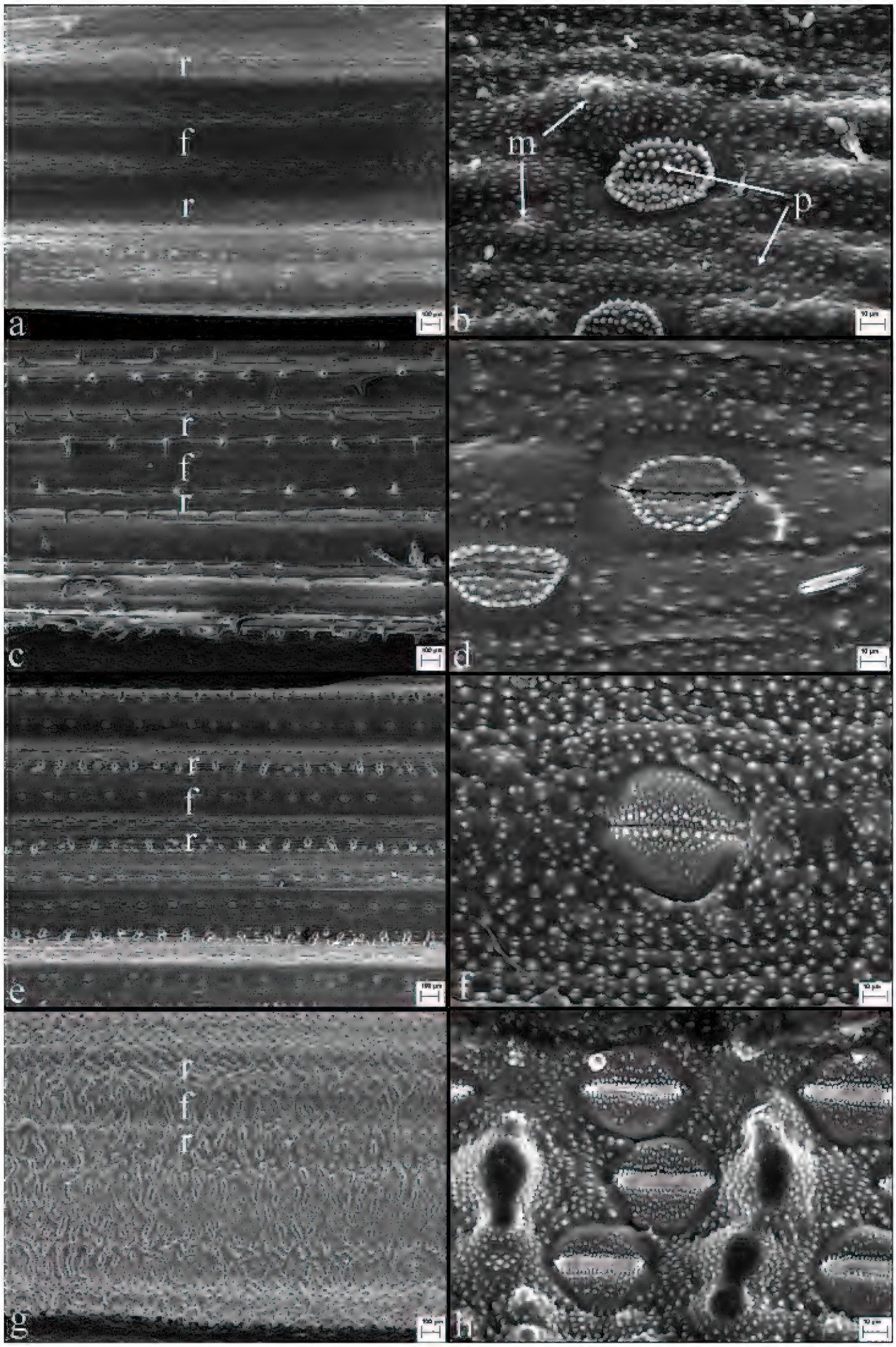

Figure 6. SEM images of the micromorphology of the shoot ridges and stomata of *Equisetum arvense* (a-b), *E. sylvaticum* (c-d), *E. pratense* (e-f), and *E. telmateia* (g-h). Arrows and letters indicate ridges (r), furrows (f), mamillae (m) and pilulae (p).

Table 1. Macro- and micromorphological characters of *E.* ×*lofotense*, *E.* ×*mildeanum* and their parent species.

	E. arvense	*E.* ×*lofotense*	*E. sylvaticum*	*E.* ×*mildeanum*	*E. pratense*
Size	(10–) 30 – 50 (–80) cm	(10–) 30 – 50 (–90) cm	(10–) 30 – 50 (–80) cm	(10–) 30 – 40 (–50) cm	(10–) 30 – 40 (-50) cm
Fertile shoot – phenology	Dimorphic	semi-dimorphic	semi-dimorphic	semi-dimorphic	semi-dimorphic
Sterile shoot – branching pattern	branches simple (sometimes with irregular secondary branches)	branches with irregular secondary branches	branches with regular secondary branches	branches with irregular secondary branches (sometimes simple)	branches simple (sometimes with irregular secondary branches)
Sterile shoot – shape	not bilaterally compressed, variable	often distinctly bilaterally compressed	bilaterally compressed only at exposed sites	often distinctly bilaterally compressed	often slightly bilaterally compressed
Sterile shoot – branch teeth	spreading away from the internode above (sometimes not spreading)	not or only slightly spreading away from the internode above	spreading away from the internode above	not spreading away from the internode above	not spreading away from the internode above
Sterile shoot – branches (length ratio of 1st branch internode to nodal sheath)	twice (or more) as long as the adjacent nodal sheath (rarely as long as)	twice as long as the adjacent nodal sheath (rarely as long as)	twice as long as the adjacent nodal sheath (very rarely as long as)	as long as to twice as long as the adjacent nodal sheath (never shorter)	slightly shorter than to as long as the adjacent nodal sheath
Sterile shoot – branches (ochreole)	green throughout	green with very short light- to reddish-brown scarious appendices	light-to reddish-brown and scarious throughout	pale green with distinct light-brown scarious appendices	pale green with short brown scarious appendices
Sterile shoot – nodal sheath	commissure distinct, of a pale green to whitish colour ridge-groove distinct	commissure distinct, of a pale green to whitish colour ridge-groove often distinct	commissure obscure ridge-groove less distinct	commissure obscure ridge-groove less distinct	commissure obscure ridge-groove less distinct
Spores	green-chlorophyllous, spherical, elater-bearing	non-chlorophyllous, irregularly shaped, without elaters	green-chlorophyllous, spherical, elater-bearing	non-chlorophyllous, irregularly shaped, without elaters	green-chlorophyllous, spherical, elater-bearing

Sterile shoot – nodal sheath (teeth)	shorter than the sheath short, dark-brown with a very small white scarious margin not or sometimes adhering together	slightly shorter than or as long as the sheath long, with a dark-brown to reddish-brown centre and a distinct white scarious margin adhering together only at the lowermost sheaths	slightly longer than or as long as the sheath long, with a reddish-brown centre and a very broad light-brown scarious margin adhering together throughout the shoot	shorter than or as long as the sheath oblong, with a brown to reddish-brown centre and a distinct light-brown scarious margin adhering together only at the lowermost sheaths	shorter than the sheath short, with a small dark centre and a broad, white, scarious margin not adhering together
Sterile shoot – micromorphology of internodes	ridges rounded silica mamillae indistinct and scattered furrows broad and rounded	ridges rounded to slightly broadened silica mamillae indistinct and scattered furrows broad and rounded	ridges broadened with two distinct margins silica mamillae thorn-like, forming two rows alongside the margins of the ridge furrows broad and rounded	ridges sharpened to slightly flattened and broadened silica mamillae 2-4, aligned, forming a single row, sometimes individually side by side furrows very small and acute, slightly broadened	ridges sharpened, hardly broadened silica mamillae 1-3, aligned, forming a single row furrows very small and acute
Sterile shoot – micromorphology of stomata (visible as two subsidiary cells)	covered with short globose pilulae density of pilulae not thinning towards the margins surface and pilulae covered with wax crystals or wax cristals absent bordered by a ring of fused pilulae pilulae at the stomatal pore globose (sometimes nearly absent)	sparsely covered with short globose pilulae pilulae only scattered, often indistinct to nearly absent surface and pilulae covered with wax crystals bordered by a ring of fused pilulae pilulae at the stomatal pore absent to indistinct globose	sparsely covered with short globose pilulae pilulae only scattered, often indistinct to nearly absent surface and pilulae densely covered with wax crystals bordered by a ring of fused pilulae pilulae at the stomatal pore absent to indistinct globose	densely covered with short globose pilulae density of pilulae not thinning towards the margins surface and pilulae covered with wax crystals ring of fused pilulae absent to indistinct pilulae at the stomatal pore globose, not stalked	densely covered with short globose pilulae density of pilulae thinning towards the margins surface and pilulae not covered with wax crystals ring of fused pilulae absent pilulae at the stomatal pore stalked with head or globose

variants of that species. However detailed differences from the parents in macro- and micromorphological aspects have been listed earlier: Page (1988; 1997), Lubienski (2003; 2009; 2013), Lubienski & Dörken (2015) (for *E.* ×*mildeanum*) and Lubienski (2010; 2013) (for *E.* ×*lofotense*). Additionally both hybrids show irregular meiotic cell division resulting in aborted spores (for images see Lubienski, 2009; 2010; Lubienski & Dörken, 2015). In both taxa a remarkable discrepancy between their macro- and micromorphological characters is expressed. Traits of the macromorphological dominant parent *E. sylvaticum* are much more obscure in the micromorphology of the main shoot of both hybrids (especially regarding the highly distinctive ridge architecture, Figures 6, 7). Macro- and micromorphological features of both hybrids and their parental species

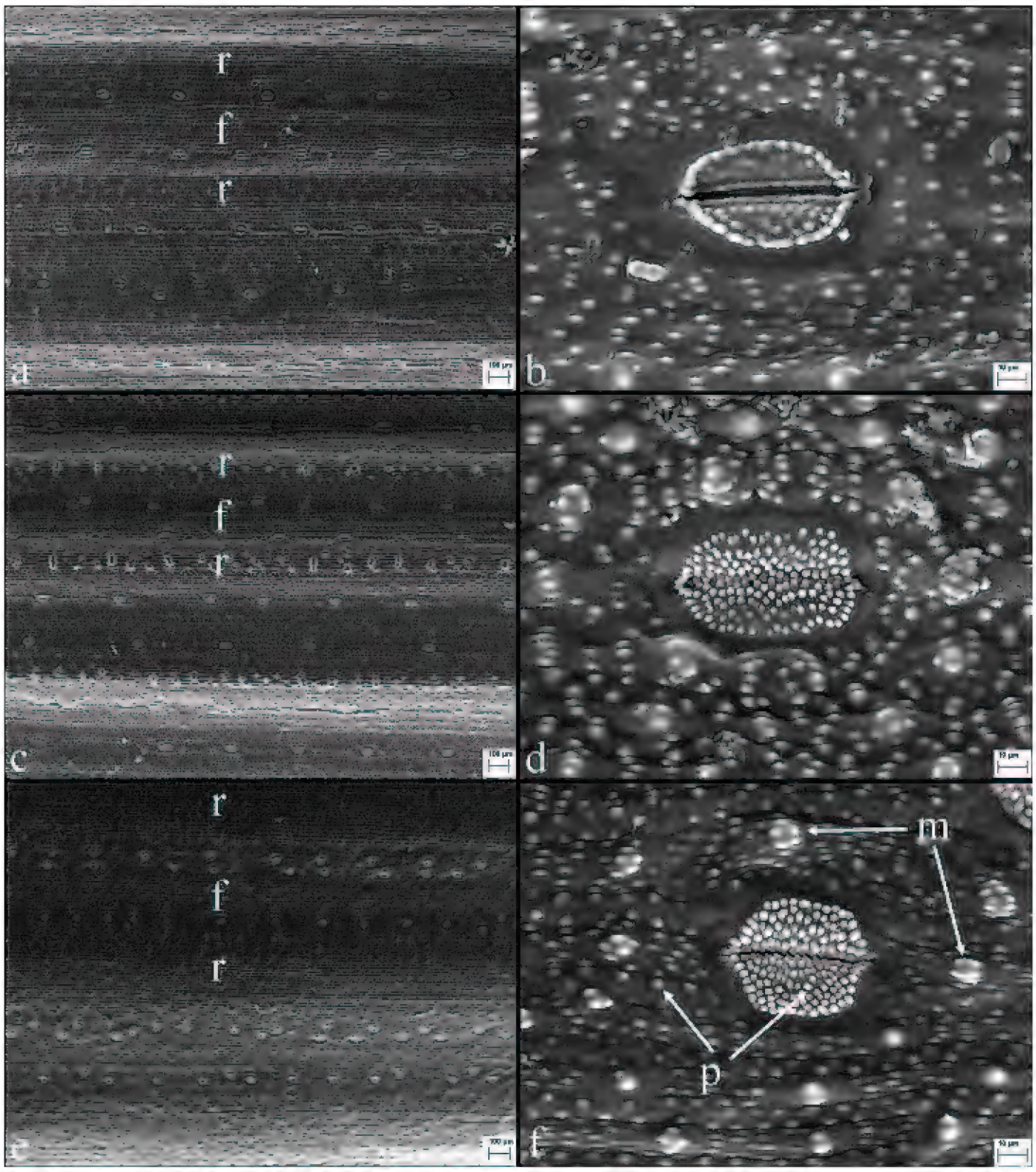

Figure 7. SEM images of the micromorphology of the shoot ridges and stomata of *Equisetum* ×*lofotense* (a-b), *E.* ×*mildeanum* (c-d), and *E.* ×*bowmanii* (e-f). Arrows and letters indicate ridges (r), furrows (f), mamillae (m) and pilulae (p).

are listed in Table 1.

The characteristic and highly distinct flattened and two-edged ridges bordered by two rows of silica spikes of *E. sylvaticum* are not found in *E.* ×*mildeanum* and *E.* ×*lofotense*. Both show a micromorphology more similar to their second parent, *E. pratense* and *E. arvense* respectively (Lubienski, 2010; Lubienski & Dörken, 2015). Interestingly this recessive behaviour of *E. sylvaticum* micromorphology is expressed to a similar degree in the third known *E. sylvaticum* hybrid, *E.* ×*bowmanii*, also a hybrid clearly indicating Wood Horsetail as one parent in its macromorphological appearance. It therefore is added in Figures 6 and 7, so that the micromorphological characters of all three known *E. sylvaticum* hybrids and their parental species can be compared directly. Because of the rarity of *E.* ×*lofotense*, in comparison with *E.* ×*mildeanum*, some further field notes of the hybrid are given, thus supplementing the data given in Lubienski (2010; 2013).

Plants on Senja were detected within the mixed stands with *E. sylvaticum*, because they displayed a characteristic asymmetric overhanging growth habit especially in the exposed roadside ditches and slopes (Figure 8a, b). In this character the hybrid is similar to *E.* ×*mildeanum* (Figure 8c, d).

Nevertheless in all dimensions it is a more robust and taller plant, reaching heights up to 90 cm (the tallest shoot found on Senja was 78 cm long, Figure 9a), which is never found in *E.* ×*mildeanum* (max. height approx. 40 cm, Figure 9b). Additionally both *E. sylvaticum* hybrids show distinctly the influence of their second parent in their nodal sheath and branch characters (Figure 10) and can be differentiated by these. An additional task in the field is to distinguish *E.* ×*lofotense* from its *E. sylvaticum* parent with which it frequently co-occurs. Differences between both are seen in the branches, the branch teeth, the sheath teeth, the shoot surface, and the fertile shoots in general.

The distinct branching pattern of all *E. sylvaticum* hybrids (Lubienski, 2010) seems to be a very stable and reliable character. The side branches are long, spreading, and secondarily branched only in their proximal part, so that a distal unbranched distinctly overhanging part results, giving the whole shoot a somehow irregular habit (Figure 11, 14b; see also image in Lubienski 2010). This differs from the very symmetric and storied branching pattern of *E. sylvaticum* resulting in brush-like side branch clusters (Figure 14a). In comparison with *E. sylvaticum* the teeth of the side branches of *E.* ×*lofotense* are not, or to a much lesser degree, spreading from the internode above (Figure 12). The sheath teeth are less reddish-brown, shorter or as long as the sheath itself (longer than the sheath in *E. sylvaticum*), only irregular adhering together, becoming darker brown, shorter and more free in the upper parts of the shoot, i.e. *E. arvense*-like. The main shoot surface is not as rough as in *E. sylvaticum*, a direct consequence of the micromorphology, where silica spikes are lacking on the less prominent ridges (Figure 7a). This difference is also clearly seen at the surface of the nodal sheath, which shows shallow ridges with a smooth surface like *E. arvense*, in contrast to prominent ridges with rough silica projections in *E. sylvaticum* (Figure 13).

The fertile shoots of *E.* ×*lofotense* have a very striking appearance at the Senja sites. These are very sturdy in general habit and bigger in all dimensions than the sterile shoots. Although this is a typical feature of the fertile shoots of all semidimorphic species and hybrids (e.g. *E. sylvaticum*, *E. pratense*, *E.* ×*mildeanum*, *E.* ×*bowmanii*), the fertile *E.* ×*lofotense* shoots from Senja are remarkable in their sturdy conifer-like habit. When viewed from above these shoots appear star-like and distinctly different from the fertile shoots of *E. sylvaticum* with which they grow intermixed. This difference results from

Figure 8. *Equisetum* ×*lofotense* (a & b) and *E.* ×*mildeanum* (c & d), showing characteristic overhanging growth habit.

Figure. 9. Shoots of *Equisetum* ×*lofotense* (a) and *E.* ×*mildeanum* (b), showing differences in size (bar = approx. 10 cm).

Figure 10. Sterile shoots of *Equisetum* ×*lofotense* (a) and *E.* ×*mildeanum* (b), showing influence of the second parent species *E. arvense* in *E.* ×*lofotense* (a) (oblong nodal sheaths and sheath teeth, low number of teeth and side branches) and *E. pratense* in *E.* ×*mildeanum* (b) (short nodal sheaths and sheath teeth, high number of densely spaced teeth and side branches).

Figure 11. Sterile and fertile shoots of *Equisetum* ×*lofotense*, showing irregular branching pattern.

Figure 12. Sterile shoots of *Equisetum sylvaticum* (a) and *E.* ×*lofotense* (b), showing differences in branch teeth, spreading (a) and not spreading (b) from the internode above.

Figure 13. Nodal sheaths of sterile shoots of *Equisetum sylvaticum* (a) and *E.* ×*lofotense* (b), showing differences in sheath surface and length and sheath teeth colour and length.

Figure 14. Fertile shoots of *Equisetum sylvaticum* (a) and *E.* ×*lofotense* (b), showing differences in branching pattern.

Figure 15 *Equisetum* ×*lofotense*, nodal sheaths, sterile (a) and fertile (b) shoot, showing different influence of the parent species *E. arvense* and *E. sylvaticum* in the macromorphological appearance of the hybrid.

the fact that the 1st order side branches of the fertile shoots of *E.* ×*lofotense* are in general longer than in *E. sylvaticum*, while having 2nd order side branches shorter than in *E. sylvaticum* (Figure 14).

Concerning the sterile and fertile shoots of *E.* ×*lofotense*, a different influence of the parent species is also expressed in the macromorphological appearance of the hybrid, making the sterile shoots more *E. arvense*-like and the fertile shoots more *E. sylvaticum*-like (Figure 15).

Distribution of *Equisetum* ×*mildeanum* and *E.* ×*lofotense*

Figure 16a shows the known distribution of *E.* ×*mildeanum* for whole Norden, and it can be presumed that other populations may be found within this area.

Figure 16b shows the distribution of *E.* ×*lofotense,* at present an endemic of northwestern Norway. Further field work in this area should explore whether it is actually more frequent than currently known. The vigour of the hybrid populations on Austvågøya and Senja makes this suggestion likely.

DISCUSSION

All four sites of *E.* ×*mildeanum* and *E.* ×*lofotense* are very similar from a geomorphological and ecological point of view, being situated within a single fjord in the north of Senja over a distance of approximately 7.25 kilometres. The habitat is exclusively a wet, north- to east-facing mountain slope characterised by huge boulders and sparse woodland, interrupted at its base by a road only a few metres above and near to the sea. All sites and the whole area in general harbour extensive stands of the parent species *E. sylvaticum*, *E. arvense* and *E. pratense*.

Horsetail hybrid colonies are often found in disturbed sites such as roadside ditches or railway embankments. This can be caused either by vegetative spreading alongside

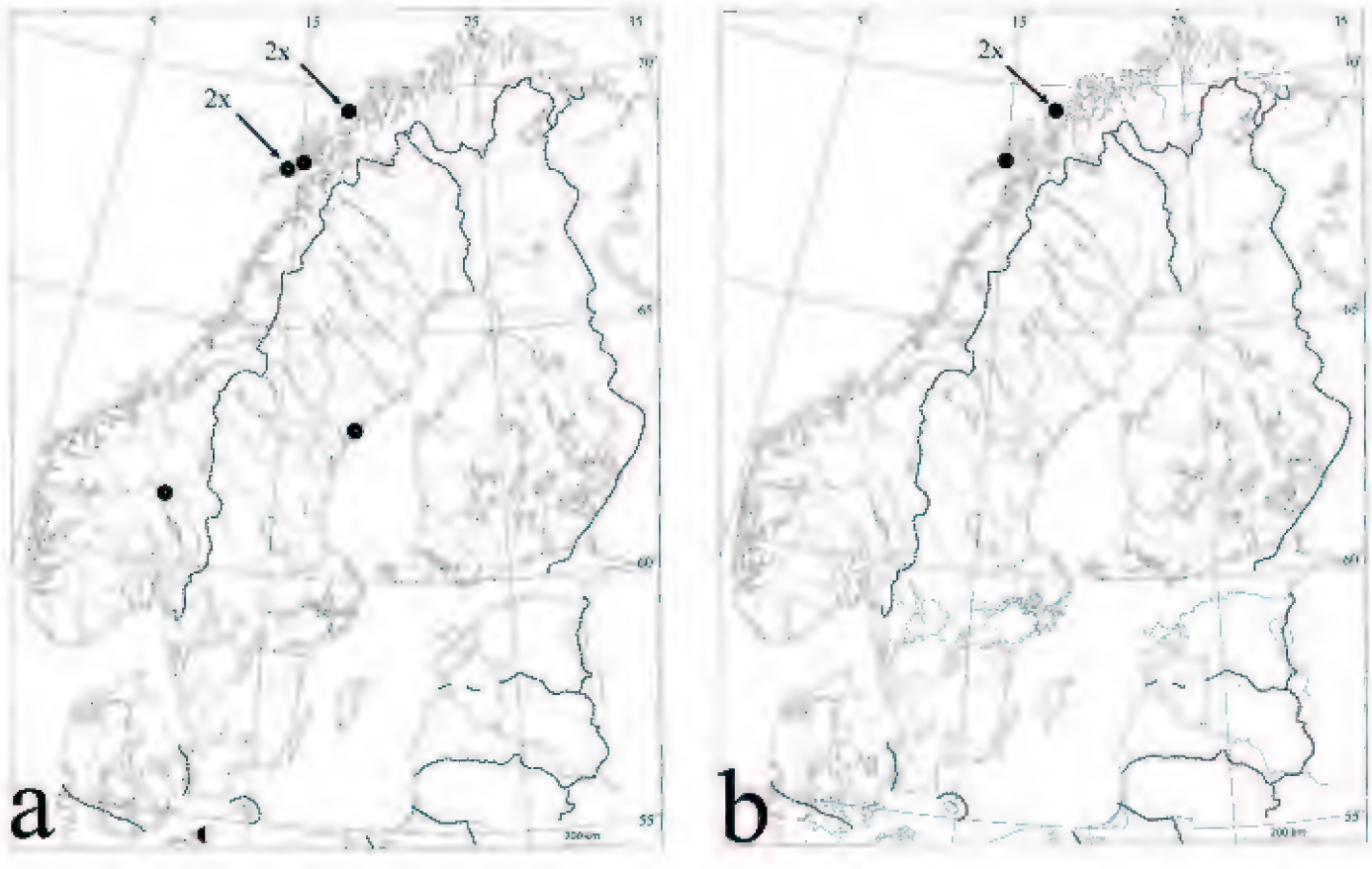

Figure 16. Distribution of *Equisetum* ×*mildeanum* (a) and *E.* ×*lofotense* (b) for Norden (arrows indicate two localities, the semi-filled dot indicates the historic occurrence of *E.* ×*mildeanum* at its type locality on the Isle of Rügen, Germany

the traffic system by rhizome or shoot cuttings or through an initial hybridization event due to ecological conditions that favour cross fertilization between *Equisetum* gametophytes. Wet roadside ditches like those on Senja display perfect conditions for germination of the chlorophyllous and short-lived *Equisetum* spores and the establishment of gametophytes. These are open raw soils without higher plant or bryophyte competition, especially after roads are periodically cleared and straightened (Hauke, 1967; Page, 1967; Duckett & Duckett, 1974; Mesler & Lu, 1977; Duckett & Duckett, 1980; Duckett, 1985). Such pioneer habitats fit with the rather narrow ecological requirements of *Equisetum* gametophytes and for this reason can harbour mixed gametophyte populations, that increase the probability of crossing events between different species (Hauke, 1978; Page & Barker, 1985; Husby, 2013).

Intergametophytic fertilization and therefore hybridization in *Equisetum* is additionally favoured by the reproduction biology of the genus in general. *Equisetum* gametophytes are initially unisexual, potentially becoming bisexual under changing growing conditions (e. g. accumulation of metabolites) (Duckett, 1972; Duckett & Duckett, 1980). However such an accumulation rarely takes place under natural growing conditions (Duckett & Duckett, 1980) and therefore bisexuality is obviously rare among wild gametophyte populations (Duckett & Duckett, 1974, 1980; Duckett, 1979). Consequently, in *Equisetum,* intergametophytic fertilization is highly effective in nature, thus outbreeding processes are facilitated. This effect is further emphasized where gametophytes of different species grow together, which in addition favours hybridization events (Duckett & Duckett, 1974; Duckett, 1979).

It seems likely that *E.* ×*mildeanum* and *E.* ×*lofotense* both originated in the roadside ditches of Mefjorden and succeeded in colonising the adjacent slopes. Each of the four colonies may have started from an individual crossing event or there may have been just two events with subsequent vegetative spread. As the two sites of *E.* ×*lofotense* are only two kilometres apart, a single *de novo* hybridization event between the parent species to form this rare hybrid seems to be most likely, followed by vegetative spread as a result of human disturbance.

Nevertheless, the fact that all four colonies stretch over at least several hundred square metres means they are unlikely to be of very recent origin.

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NEW RECORD OF THE RARE *SERPOCAULON OBSCURINERVIUM* D. SANÍN (POLYPODIACEAE) IN THE EASTERN CORDILLERA OF COLOMBIA

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Key words: Andean-Amazonian foothills; Caquetá; Huila; ferns; Florencia; distribution range; epipetric habit.

ABSTRACT

Serpocaulon obscurinervium is considered as a rare and threatened species, with only four exemplars registered including the type. It was recorded from Colombia and Ecuador, but most commonly reported for central southern Colombia (central west of Chocó and south of Nariño departments). Here, we expand its distribution by reporting new records for this species on both sides of the Eastern Cordillera of the Colombian Andes, specifically from the high Andean forest of Florencia, in the Caquetá department and Suaza in the Huila department. Furthermore, this is the first record of the species as an epipetric plant. Pictures of the plant and an updated distribution map are provided.

INTRODUCTION

Serpocaulon A. R. Sm. (Polypodiaceae) is a neotropical fern genus, which contains 52 taxa (Sanín 2015). These species occur mainly in humid forests (Smith et al. 2006). Colombia harbours 27 species that are distributed in the inter Andean valleys, the Chocó Region, the Sierra Nevada de Santa Marta, Oriental valley and Amazon, but most species occur in the humid forests of the Andes and the Chocó Region (Sanín in press).

Serpocaulon obscurinervium D. Sanín (Figure 1) is an Andean species that was described in 2014 from herbarium specimens deposited in collections of Colombia (CHOCO, COL, CUVC and PSO), France (P) and United States (MO and UC) (Sanín 2014). The first specimen was collected in Ecuador by R. Spruce in 1909. In 1973, other specimens were collected in Nariño at 2500m by O. Hagemann & L. Leist. The most recent collections were recorded in 1988 in the Andean zone of the Department of Chocó by P. Silverstone–Sopkin, and in La Planada Reserve, Nariño Department, by H. Herrera

(Sanín 2014). Because the distribution of the species within Colombia was restricted to high montane forests outside of any protected area, its conservation status was considered as Endangered (EN) following the IUCN criteria (Sanín 2014). Since its first description, the species had never been found again or reported alive in nature.

During the ongoing botanic exploration of the Caquetá and Huila departments, *Serpocaulon obscurinervium* was recorded growing in sites on both sides of the Eastern Cordillera. The specimens were found along the roadside of Puente Cerro Negro in El Portico, at the western slope in a forest at 2190m and in Gabinete military station at 2050m on the border of Caquetá and Huila Departments on the Eastern slope of the Eastern Andean Cordillera. In Huila Department, it was also found on the road to Neiva, in the municipality of Suaza at 2190m (Figure 2). Two to five vouchers were collected per site and were deposited at the following herbaria: CAUP, COAH, COL, HUA, FAUC & PSO.

The exemplars from Caquetá (Puente Cerro Negro and Gabinete) are the first records of *Serpocaulon obscurinervium* as an epipetric fern. In addition, it is the first time that the species has been collected in the Caquetá and Huila departments (Murillo-P. et al. 2016), the easternmost distribution of the species with its nearest known population at

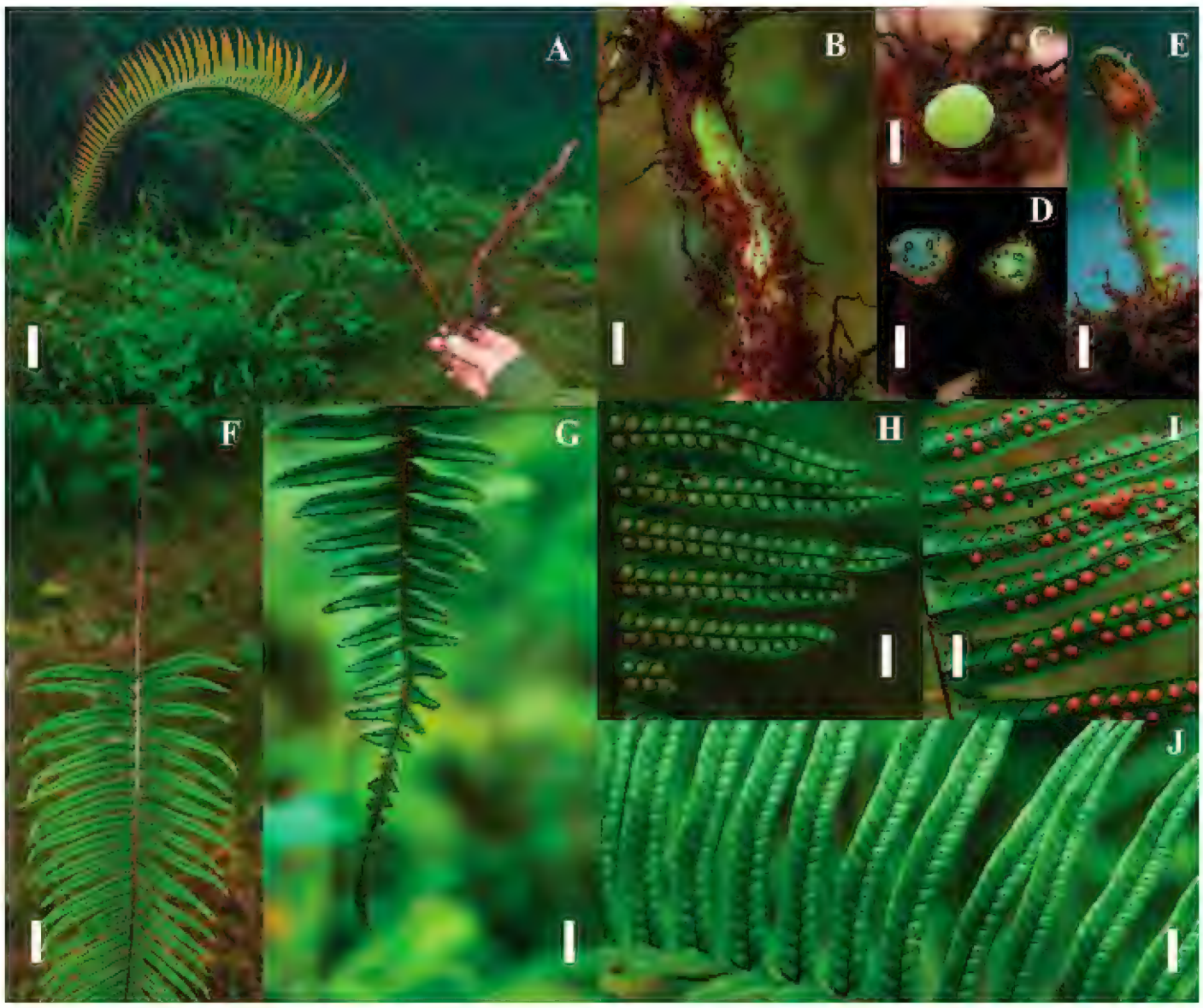

Figure 1. *Serpocaulon obscurinervium*. **A:** Habit of the plant, scale bar (5 cm). **B:** Rhizome, scale bar (1 cm). **C:** Rhizome bundles, scale bar (3.5 cm). **D:** Petiole bundles, scale bar (2 cm). **E:** Fiddlehead, scale bar (1 cm). **F:** Lamina base, scale bar (3 cm). **G:** Lamina apex, scale bar (3 cm). **H:** Immature sori, scale bar (8 cm). **I:** Mature sori, scale bar (8 cm). **J:** Pinna veins, scale bar (8 cm). All from *Sanín & Peña 6371* (COL, HUA). Photos by J.L. Peña.

250 km distance on the road of La Victoria−Monopamba, Dept. Nariño, in central south Colombia.

Serpocaulon obscurinervium is closely related to *S. eleutherophlebium* (Fée) A. R. Sm., a species that is distributed from Costa Rica to Ecuador and Venezuela (Moran 1995, Smith et al. 2006), and in Colombia is widely recorded in high Andean forest and

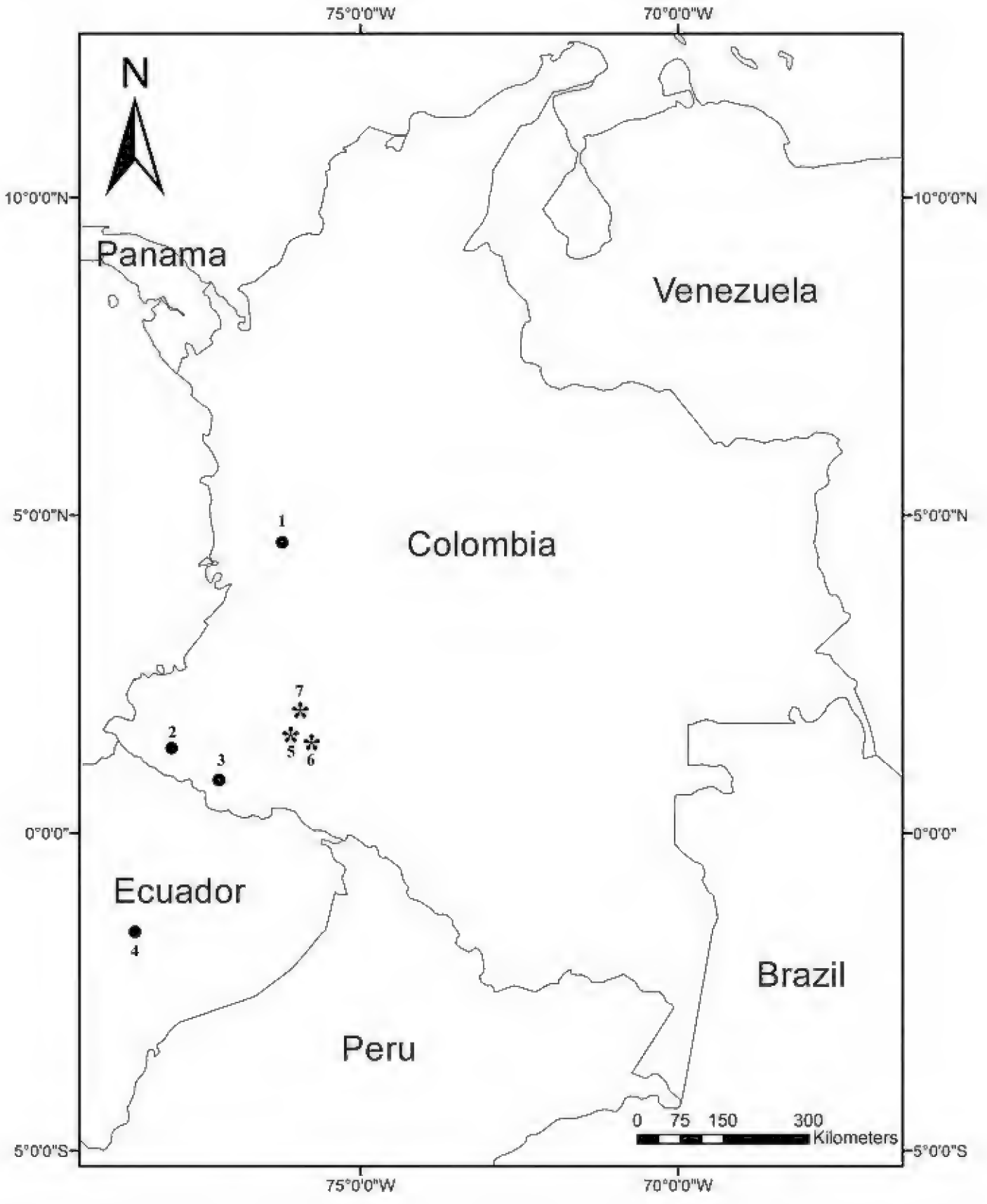

Figure 2. Distribution of *Serpocaulon obscurinervium*. The black dots are previous registers of the species: **1)** Cerro del Torrá, Valle del Cauca, Colombia; **2)** La Planada Reserve, Nariño, Colombia; **3)** road La Victoria−Monopamba, Nariño, Colombia; **4)** Tungurahua, Mt. Abitagua, Ecuador. The asterisks are the new registers on the Oriental Andean Cordillera of Colombia: **5)** El Portico and **6)** El Gabinete from Florencia, Caquetá department and **7)** From Suaza, Huila department.

subpáramos at 2430-3950m, epiphytic, terrestrial and rupicolus (Sanín in press).The identification of these two taxa has been confused. Both species have similar long-creeping rhizomes, scales with patent apices, concolorous and pinnatisect laminae. However, *S. obscurinervium* differs from *S. eleutherophlebium* in the scales characters, being linear-lanceolate (versus subulate), dark orange (versus dark brown), larger sized 5.2-(6.3)-8.5 × 1.6-(1.7)-2.3 mm (versus 3.5-(5.1)-7.1 × 0.5-(1.1)-1.7 mm), and with longer petioles 24-(2.6)-28 cm (versus 3.4-(12)-25.5 cm), more areoles along the middle segment 19-(20)-28 rows (versus 6-(12)-21 rows), inconspicuous fertile veinlets (versus conspicuous fertile veinlets), and the presence of 2-4 celled, dispersed, catenate, terete and dark brown trichomes on the blades and rachises (versus absent trichomes) (for a complete comparison see Sanín 2014).

Even though three more populations of *Serpocaulon obscurinervium* were discovered in the Caquetá and Huila departments, it is still categorized as Endangered [EN B1ab(i, ii, iii) + B2ab(i, ii, iii)] following the IUCN criteria. Here we present more support for this, and include Criterion D to its IUCN categorization: [EN B1ab(i, ii, iii) + B2ab(i, ii, iii) + D], the latter given that the population size of *S. obscurinervium* is estimated to be fewer than 250 mature individuals.

The sparse and vicariant distribution of the species on the Andean Cordillera of Ecuador and Colombia (Sanín 2014), and the reduction of high montane forest vegetation caused by human settlements and agricultural expansion (Murcia et al. 2010), impose a permanent and increasing danger to the populations of this species, especially as all the records of this species are outwith any protected area. In addition, from five to 10 individuals were recorded in these new localities, including both mature and juvenile individuals (pers. obs.).

MATERIAL EXAMINED

***Serpocaulon obscurinervium*—Caquetá**: Florencia, Via Neiva, vereda El Condor, a mano derecha de la vía, a 100m del Puente Cerro Negro [1°45'19.62" N , 75°44'59.98" W], 2050m, 27 Jul 2015, *Sanín & Peña* 6371 (CAUP, PSO, COL, HUA); Florencia, Via Guadalupe, El Gabinete, a mano izquierda de la vía, a 100m de la estación militar [75º40'58.4" O, 1º52'44" N], 2700–2800m, 20 Feb 2016, *Sanín, García & Camargo-García 6396* (COAH, COL, FAUC, HUA); **Huila**: Suaza, via Neiva, vereda Campo Hermoso, costado izquierdo de la via, km 40 [1°46'11.71" N, 75°46'37.52" O], 2190m, 1 Apr 2016, *Peña* 542 (COL) **Chocó:** San José del Palmar, Cerro Torrá, Filo de Cumbre, [04º48' N, 76º29' W], 2700–2800m, 21 Aug 1988, *Silverstone-Sopkin* 4633 (Paratypes: CHOCO, CUVC, MO, UC n.v.). **Nariño:** Reserva Natural La Planada, sendero entre El Hondón y Los Horquetas, Bosque primario, 01º10' N, 78º00' W, 1820m, 31 Jan [no year given], *Herrera* 9302, 9193 (Paratypes: PSO, CUVC, UC n.v.); Carretera La Victoria–Monopamba, [01º10' N, 78º00' W], 2500m, 10 Jan 1973, *Hagemann & Leist 1898* (holotype: PSO; isotype: COL).

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POLYSTICHUM LONCHITIS (DRYOPTERIDACEAE: PTERIDOPHYTA) A MONTANE-ALPINE FERN SPECIES, MONITORED SINCE 1978 IN THE NETHERLANDS

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Key words: *Polystichum lonchitis*, Kuinderbos, monitoring, mortality

ABSTRACT

Polystichum lonchitis was found in 1978 for the first time in The Netherlands on a dry ditch bank, on calcareous sand within a planted woodland (Kuinderbos). In subsequent years six other specimens were found at three other sites, in a woodland, on a scree in a chalk stone quarry and on a wall, and four of these plants became fertile. Mortality in five out of seven plants resulted from a small landslide, habitat destruction, browsing and frost damage. Long term monitoring of two plants showed the impact of rainfall and frost on vitality. No recruitment was observed in the spore shadow of adult plants.

INTRODUCTION

Polystichum lonchitis (L.) Roth. is a montane-alpine species, with a Holarctic distribution. In North America it is a species found mostly in boreal and subalpine regions between 0 and 3200 m (Morin, 1993). In Europe the species is found between 900 and 2100 m and rarely at lower altitude up to 300 m, except for the coastal area of Norway (Mutter *et al.*, 1998). It is also found in Greenland, Iceland and in isolated parts of Russia but is rare in Japan (Dostál & Reichstein, 1984). Within the UK it is more widespread in the central Scottish Highlands (c. 610 – 915 m). Occasionally it descends to lower altitudes in steep upland river valleys (c. 150 m) and lower levels near the west coast, with its cool summers (Page, 1982). In 1978, *Polystichum lonchitis* was recorded for the first time in the Netherlands during a survey of 120 km of dry ditches in the Kuinderbos. Two plants were found growing at the sides of two adjacent dry ditches on the bottom of the former Zuiderzee at ca. 1 m below sea level (Bremer, 1980). Since then this small population has been monitored annually for the first 15 years and less intensely in subsequent years. After 1979 the species was found at three other sites in the Netherlands, and monitored annually near Lelystad (Smit, 1989). This paper analyses these records to try to determine whether a montane-alpine plant species is able to build up a viable lowland population.

METHODS

Two plants (plant 1 and 3, both in Flevoland, Table 1) were monitored for 24 years (Kuinderbos) and 27 years (Lelystad) with annual counting of the number of fronds and the maximum frond length and fertility at the end of the summer season or start of autumn, when frond formation had stopped and sori produced. Change in maximum frond length, change in number of fronds and the log transformed product of both parameters (always year t to year t + 1) were used as response variables to rainfall and the number of frost days. The average values in Flevoland were used for annual rainfall

Table 1. Some characteristics of the Dutch population of *Polystichum lonchitis*. Nr = plant number, as mentioned in the paper. First = first year of recording, Last = last year of recording, year of death. Fer = Fertility of plant: 0 = not fertile, F = fertile during period of recording, ? = not known, Sl = slope in °, Asp = aspect, Tree layer: Fr = *Fraxinus excelsior*, Qu = *Quercus robur*, Cb = *Carpinus betulinus*. Mo = cause of mortality: Ls = small scale land slide, Hd = habitat destruction, Fd = frost damage, Br = browsing .

nr	Location	First	Last	Fer	Leg	habitat	Substrate	Sl	Asp	Tree layer	Mo
1	Kuinderbos	1978	2014	F	P. Bremer	ditch side, woodland	fine sand	62	NE	*Fr*	*Ls*
2	Kuinderbos	1979	1984	F	P. Bremer	ditch side, woodland	fine sand	80	SW	*Fr*	*Ls Fd*
3	Lelystad	1986		F	A. Smit	ditch side, woodland	sandy clay	45	SSW	*Fr-Qu*	
4	Vlaardingen	1994	1994	0	B. van As	wall	cement	90	E	-	*Hd*
5	`t Rooth	1998	2011	?	J. Egelsmeer	quarry	loamy soil on chalk	45	N	-	*Br, Fd*
6	`t Rooth	1998	1998	0	J. Egelsmeer	quarry	loamy soil on chalk	>30	N	-	*Hd*
7	Kuinderbos	2011		F	P. Bremer	ditch side, woodland	fine sand	40	SW	*Fr,Cb*	

Table 2. Correlation matrix with doses and effect parameters with correlation (r) and significance (p) shown (and significant levels $p < 0.05$ marked with asterix *). ▲ n = change in number of fronds between year t and t + 1, ▲ Fm = change in maximum frond length between year t and t + 1

Plant 1, Kuinderbos

		▲ n	▲ Fm	▲ (nxFr)	log ▲ (nxFr)
Rainfall year t	r	0.1	0.01	0.77	-0.01
	p	0.67	0.96	0.75	0.96
Rainfall April year t+1	r	0.33	0.2	0.37	0.17
	p	0.17	0.41	0.12	0.5
Rainfall May-July year t+1	r	0.62	0.17	0.42	0.61
	p	0.01*	0.49	0.07	0.01*
Rainfall May-July year t	r	-0.14	0.19	0.14	0.14
	p	0.95	0.43	0.58	0.58
Number of frost days	r	-0.25	-0.4	-0.32	-0.23
	p	0.3	0.09	0.18	0.34

Plant 3, Lelystad

		▲ n	▲ Fm	▲(nxFr)	log ▲ (nxFr)
Rainfall year t	r	-0.43	0.02	-0.36	-0.28
	p	0.03*	0.93	0.07	0.17
Rainfall April year t+1	r	0.2	0.08	0.16	0.21
	p	0.32	0.7	0.44	0.31
Rainfall May-July year t+1	r	0.09	0.42	0.22	0.27
	p	0.66	0.03*	0.29	0.17
Rainfall May-July year t	r	-0.38	-0.11	-0.32	-0.39
	p	0.06	0.58	0.11	0.05*
Number of frost days	r	-0.12	-0.45	-0.28	-0.28
	p	0.56	0.02*	0.17	0.16

in year t, rainfall in April in year t + 1, rainfall in May-July in year t and t + 1, as we expected drought in spring or early summer to play a role. The number of frost days per winter (maximum day temperature below 0°C) was used as indicator for the low temperature impact in winters regional data used (www.knmi.nl). These were the same parameters as used by Bremer & Jongejans (2010) in their study on the demography of *Asplenium scolopendrium* L. SPSS 10.1 was used to calculate correlations. Per location data about habitat, substrate, inclination, aspect and composition of the tree layer and herb layer were collected in order to classify the sites and vegetation.

RESULTS

Habitat and vegetation

Over a period of 39 years seven plants were found at the former sea floor in Flevoland, in the city of Vlaardingen and in a chalk quarry in the southern part of the Netherlands (Figure 1). The Kuinderbos plants grew in dry ditch sides within plantations of *Fraxinus excelsior* L., accompanied by mosses of the *Fissidentietum taxifolii* bryophyte community (Bremer, 1999) and fern species such as *Asplenium scolopendrium* and *Polystichum aculeatum* (L.) Roth. Near Lelystad the plant grew under a canopy *of Fraxinus excelsior* L., with *Oxyrhynchium hians* (Hedw.) Loeske, *Eurhynchium striatum* (Hedw.) Schimp. and *Geum urbanum* L. The non-native *Potentilla indica* (Andrews) Wolf had invaded the site. This vegetation is related to the *Fraxino-Ulmetum*, a woodland community confined to clayey soils in the Netherlands. Both `t Rooth plants were found growing among flint stones deposited at a chalk quarry. The vegetation at this site was characterized by mass growth of *Asplenium trichomanes* L., *Gymnocarpium robertianum* (Hoffm.) Newman and *Asplenium scolopendrium*. In the bryophyte layer *Encalypta streptocarpa* Hedw. was a prominent species. Even *Asplenium ruta-muraria* L. was growing among flint stones, one of the few examples where it shows terrestrial growth in the Netherlands. The vegetation belongs to the *Asplenietum ruto-murario-trichomanes*, a community strongly linked to wall habitats (Segal, 1969) (OV39, British National Vegetation Classification, Rodwell, 1992). The Vlaardingen site was by a wall, which was destroyed two years after the discovery of *Polystichum lonchitis*. The vegetation belonged to the *Filici-Saginetum*, a wall community with *Dryopteris filix-mas* (L.) Schott and *Asplenium scolopendrium*. All sites have a high pH in common and are related to gradients. There was no difference in aspect comparing N-NE with S-SW ($\chi^2 = 0.14$ ns) (Table 1).

Distribution and trend

The number of plants varied from one to two plants per location. The small population in the Netherland showed a positive trend until 2010 with decline in recent years (Figure 2). Most plants were found as adults; the Vlaardingen plant was a juvenile/subadult plant, rather small in size, as is often the case with wall dwelling fern species. Five plants died because of landslip, habitat destruction, frost damage and browsing or because of a combination of these factors (Table 1). At Vlaardingen, prior to wall destruction, the plant was conserved and planted in a garden but was subsequently lost through theft within two years. At `t Rooth quarry one of the sites was destroyed in favour of pond digging because of a threatened toad species. The other plant died as a result of browsing in combination with frost damage (Bremer & Egelsmeer, 2015). In the Kuinderbos, one plant slipped to the bottom of the dry ditch after a small scale land slip (initiated by heavy rain fall) and drowned as the normally dry ditches contain water (0.1 – 0.3 m depth) in

winter time. Four out of seven plants became adults, producing spores nearly every year. No recruitment took place in the spore shadow.

The impact of severe winters and rainfall

The first plant found in the Netherlands (Kuinderbos, plant number 1) has been monitored since 1979. The maximum frond length (Lm) increased exponentially between 1979 and 1985. During the severe winter of 1984 - 1985 it was not harmed at all; number of fronds and maximum frond length increased, despite 22 frost days during that winter. The winter 1985 - 1986 was also long and cold, with the same number of frost days as in the

Figure 1. Distribution of *Polystichum lonchitis* in the Netherlands with number of plants per location (small dot = 1 plant, larger dot = 2 plants). The Kuinderbos is at 52°46` N 5° 49`E.

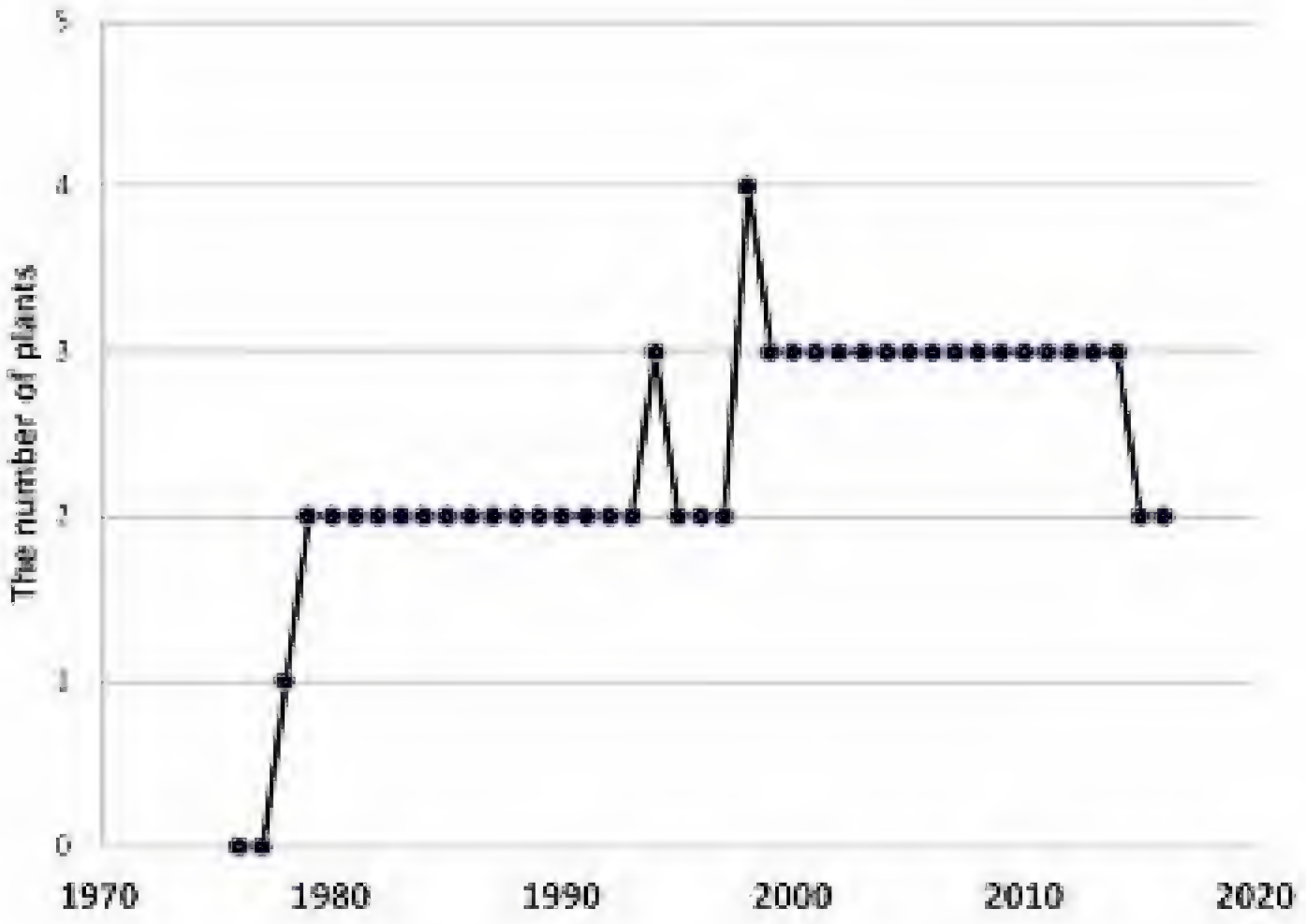

Figure 2. The number of plants during half a century in The Netherlands since 1978.

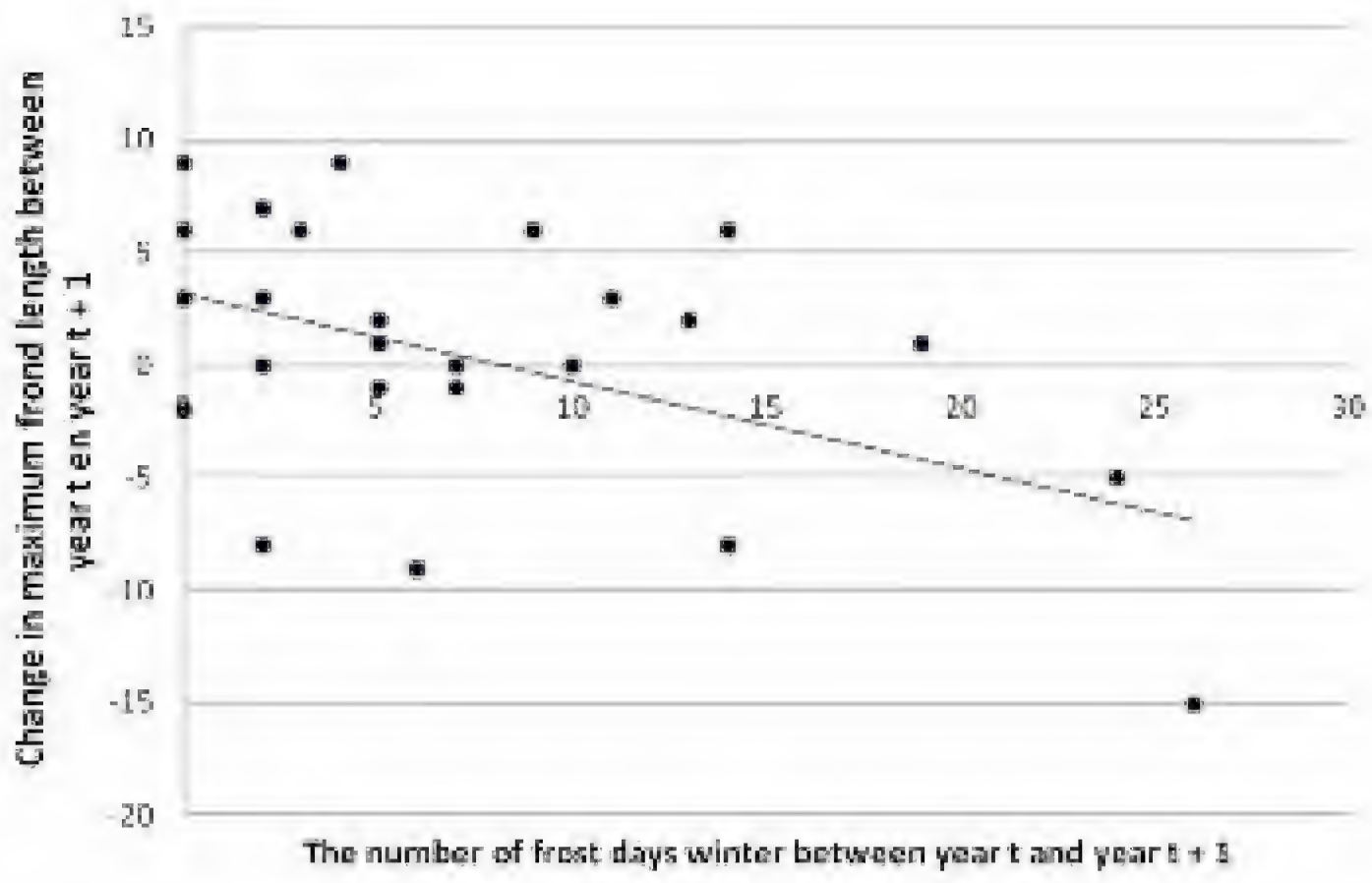

Figure 3. The change in maximum frond length between year t and year t + 1 related to the number of frost days per winter between year t and year t + 1 in the Lelystad plant. (plant number 3).

preceding winter. The plant produced fewer and smaller fronds and the plant was sterile for one year. In subsequent years the plants recovered. Over the whole period the vitality parameters in plant 1 did not correlate significantly with the number of frost days (Table 2). The Lelystad plant however showed a significant negative correlation between change in frond length and the number of frost days per winter ($n = 26$, $r^2 = 0.18$ $p = 0.03$) (Figure 3).

When analysing rainfall and growth a positive correlation was found in Kuinderbos plant 1 between the change in number of fronds and the May-July rainfall in the year t + 1 ($n = 19$, $r^2 = 0.38$ $p = 0.01$) (Figure 4) and in plant 3 (Lelystad, Figure 5) between the change in frond length and May-July rainfall in year t + 1 ($n = 26$, $r^2 = 0.18$, $p = 0.03$). The log transformed product of the change in maximum frond length x change in number of fronds showed a strong correlation in plant 1 ($n = 19$, $r^2 = 0.36$, $p = 0.01$). The annual rainfall had a negative impact on plant 3 ($n = 26$, $r^2 = -0.16$, $p = 0.03$).

DISCUSSION

The site in `t Rooth is an artificial flint stone scree in a chalk quarry, which resembles the more natural habitat. In Scotland stable boulder scree slopes may contain a rich fern vegetation with *Asplenium viride* Huds., *Cystopteris fragilis* (L.) Bernh and *Dryopters expansa* (C.Presl) Fraser-Jenk.& Jermy (Page, 1982). On ledges it grows among low-growing flowering plants in the *Dryas octopetala – Silene acaulis* ledge community (Rodwell, 1992). Probably the dry ditches under a canopy can at best be compared with the gryke habitat - fissures in exposed limestone habitat that are usually 1 – 2 m deep (Lake *et al.*, 2015). From the syntaxonomical point of view the woodland sites have

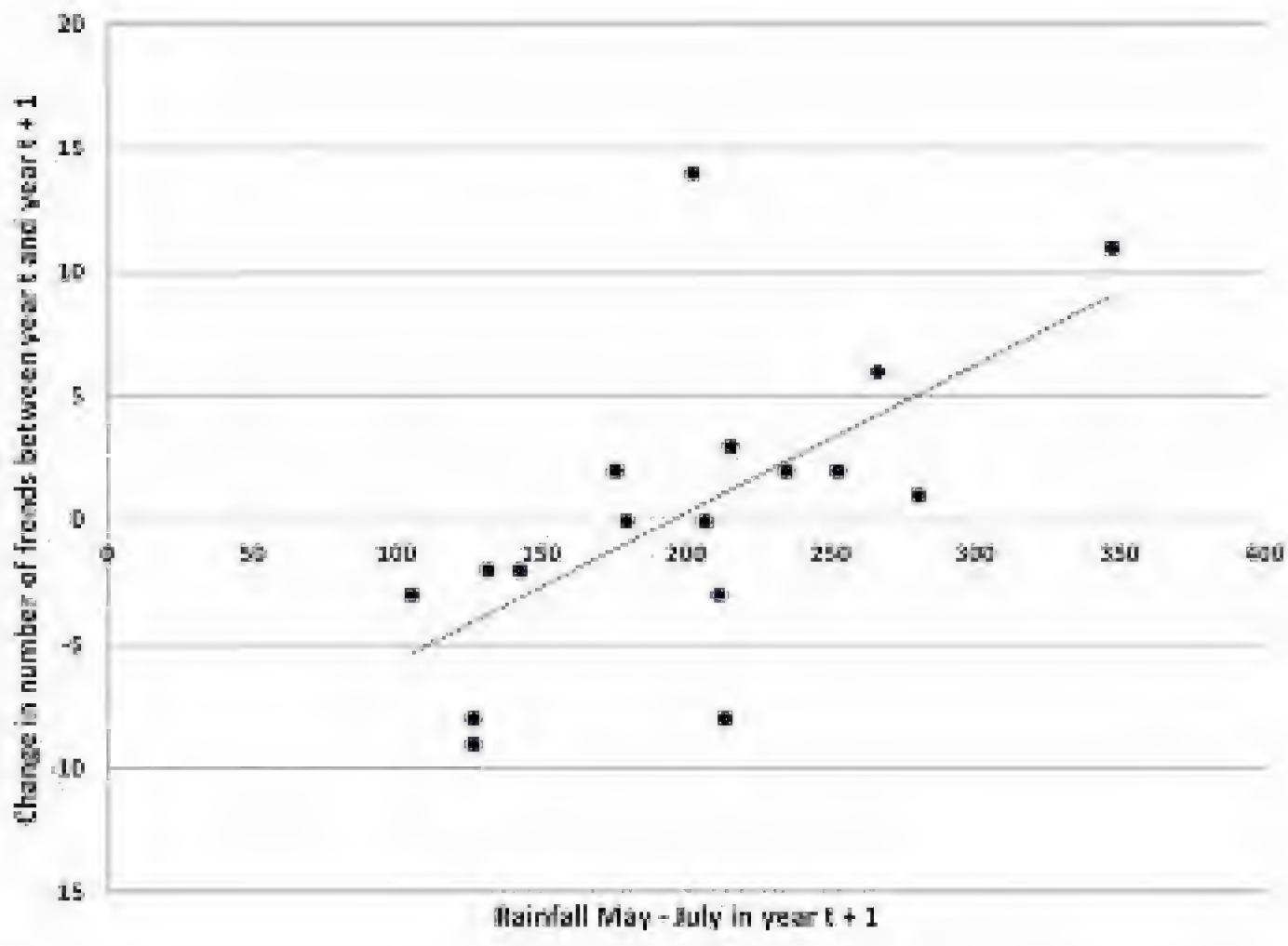

Figure 4. The increase of number fronds (year t and year t + 1) related to the rainfall in the period May – July in year t + 1 in the Kuinderbos plant (plant number 1).

Figure 5. The Lelystad plant (plant number 3) accompanied by *Potentilla indica* in 2007, 21 years after the first record (photo P. Bremer)

Figure 6. The plant recorded in the Kuinderbos in 2015 (plant number 7), first discovered four years after the first record (photo P. Bremer).

much in common with, the *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland and in particular the *Geranium robertianum*-subcommunity, where sometimes it is found under a miniaturised version of this woodland in the Carboniferous Limestone grykes in the Yorkshire Dales (Rodwell, 1998).

The montane-alpine species was not expected to colonise a former sea floor. In neighbouring countries lowland sites for this species are not known (e.g. www.floraweb.de). In the year *Polystichum lonchitis* was recorded for the first time, *Asplenium viride* Huds. was also found in the Kuinderbos (Bremer, 1981), and some montane bryophytes had been found on dry ditch sides on the former seafloor [e.g. *Distichium inclinatum* (Hedw.) Bruch & Schimp. (Bremer & Ott, 1979) and fungi (e.g. *Suillus tridentinus* (Bres.) Singer]. The Kuinderbos is the only known site within the Netherlands with a small viable population of the montane *Knautia dipsacifolia* Kreutzer (Meijer & Bremer, 1986). All these species came by long distance dispersal by wind, with *Knautia dipsacifolia* being the exception (probably with humans as vector).

Page (1982) states that the species occasionally descends to lower altitudes near the extreme west coasts of Scotland because of its cool summers. At open sites in the Netherlands the preferred N-E aspect was confirmed. In the Dutch woodlands it thrives with a SW preference, although in April, without the protection of a sprouted canopy, it can be warm in these ditches. A high temperature is probably compensated by evaporation of water, as dry ditches always contain water in this time of the year.

There is a continuous flow of diaspores from mountainous areas spreading over the Netherlands, implicating that under optimal conditions plants can establish from spores. But the chance of establishment is dependent on the extent of an area which is suitable for colonisation, spore density, spore longevity (sporebank) and the ability of intragametophytic selfing (Klekowski 1979). In the Kuinderbos 300 ha of calcareous deposits on peat drained by more than 100 km of dry ditches provided a large area, with colonization by numerous rare fern species (Bremer 2007, de Groot 2012). De Groot (2012) showed in four species [*Asplenium scolopendrium*, *A. trichomanes*, *Polystichum aculeatum*, *P. setiferum* (Forssk.) Woynar] a very high selfing capacity in both diploid and polyploid species. Single-spore establishment following long-distance dispersal may have resulted in selection for selfing genotypes. There was no recruitment from the adult plants of diploid *Polystichum lonchitis*, at woodland sites. This might indicate that selfing is less likely in a second generation and that the species depends on intergametophytic crossing. There is a very low chance that spores from other genotypes are able to establish within the spore shadow of an adult plant because of the large distance to British and Central European populations. *Polystichum lonchitis* does have Arbuscular Mycorrhiza (Harley & Harley, 1987), but it is unknown whether fungi play a crucial role in establishment. With only two plants left, stochastic extinction might occur. In the Netherlands Atlantic species such as *Asplenium scolopendrium, Dryopteris borreri* Newman, *D. affinis* (Lowe) Fraser-Jenk. and *Polystichum setiferum* are increasing in number and becoming more common. Global warming with more precipitation in summer and higher temperatures in winter plays a role. With its fluctuating small population *Polystichum lonchitis* remains a threatened species on the Dutch Red List (Sparrius *et al.*, 2012). Landslip within dry ditches, frost damage, habitat destruction and browsing played a role in the mortality of five out of seven plants. One plant lived for ca. 45 years. Northridge writes that one of five Fermanagh plants (N. Ireland) was found as a mature plant in 1979 and was still in excellent condition 32 years later (www.habitas.org.uk/priority/species). Although plants in the UK seem to be long-lived,

no demographic studies are known for this species. In the Netherlands frost damage played a role in vitality and survival. One would expect a montane-alpine species to more adapted to low temperatures, yet effects of severe winters were observed in four of seven plants, with plants becoming smaller, with lower number of fronds per plant, smaller fronds per plant or lower fertility. The same was observed in *Asplenium scolopendrium*, but this species has an Atlantic distribution, and is susceptible to frost. In this species snow cover can protect plants from heavy damage (Bremer & Jongejans, 2010). The more leathery fronds of *Polystichum lonchitis* (see Figure 6) seem to be more protective than those of *Asplenium scolopendrium*. However, our data suggest that snow cover might be crucial, a suggestion also made by Dostál & Reichstein (1984), indicating growth in snow-rich habitats. Mutter *et al.* (1998) did not find a role of extensive snow cover. For many subalpine species snow cover is a prerequisite for survival during winters (Körner & Larcher, 1988) as snow protects from low temperatures. Buried beneath a layer of snow plants are exposed to milder temperatures close to 0°C. Without snow cover desiccation plays a role or excessive natural radiation may result in frost damage. As old fronds might serve as nutrient storage organs frost damage impacts the new generation of fronds (Landi *et al*., 2014).

Within the Netherlands long term monitoring of a complete plant population is exceptional. While in other groups, e.g. breeding birds, annual monitoring is commonplace, it is much more difficult in plants. Individuals in many species are more difficult to identify [e.g. *Pteridium aquilinum* (L.) Kuhn] and a complete survey of a large area time consuming. Plant species involved mostly have a restricted number of populations, as is the case in *Woodsia ilvensis* (L.) R.Br. (McHaffie, 2010) and more long term monitoring in ferns is needed (Sharpe & Mehlteter, 2010).

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BOOK REVIEW

An Annotated Checklist of Indian Pteridophytes Part – 1 (Lycopodiaceae to Thelypteridaceae. Fraser-Jenkins, C.R., Gandhi, K.N., Kholia, B.S. & Benniamin, A. 2017. pp 562. Bishen Singh Mahendra Pal Singh, Dehra Dun, India.

This new checklist of Indian pteridophytes is a welcome addition to our knowledge of the diversity of Asian ferns and lycophytes, and adds to the recent publications on pteridophytes from China (Wu et al. 2013) and Nepal (Fraser-Jenkins et al. 2015). This volume covers Indian Lycopodiaceae, Selaginellaceae, Isoetaceae, Equisetaceae and 19 fern families (Psilotaceae to Thelypteridaceae).

In addition to the detailed checklist that forms the bulk of the volume, there is a short introduction that sets the work in context and a summary of the numbers of families, genera and species that are to be included in both Parts 1 and 2. The checklist itself is followed by a series of 37 colour images, that range from some significant herbarium specimens to many field photographs of living plants, either in close-up or as habitat shots, and all of these providing a beautiful visual introduction to the vast range of diversity among Indian pteridophytes.

In generating the information for this detailed checklist, the authors have combined an extensive literature review with detailed studies of herbarium specimens and distributions from both public and private herbaria from India and elsewhere, and sound field knowledge. Critical comparison has been made with records from adjacent areas, and this has led to the inclusion of 34 families, 130 genera, 1107 species and 50 additional subspecies for the whole of the checklist, of which 23 families, 59 genera, 572 species and 32 additional subspecies are covered in Part 1. In addition, for each of the genera, the authors provide lists of excluded taxa; this is very valuable in clarifying the presence/absence of taxa for which past records have proved to be erroneous, often the result of confusion of nomenclature.

The new checklist has a traditional taxonomic framework; the authors have considered recent taxonomic approaches built on phylogenetic analysis of DNA sequence data but have given greater weight to morphological classification. One of the strengths of this checklist is in the detailed citations for families, genera and species, including citation of types and synonyms, and information on distribution within and outwith India. For many of the species there are extensive notes to clarify previous reports, to point out mis-identified material or instances where there has been mis-application of names, sometimes in attempted lectotypification. This detailed clarification of the names used (and those excluded) in the checklist is invaluable for other researchers, and comparison can be made with, for example, fern taxa from elsewhere in Asia.

In a taxonomic work of this detail it is not surprising to find that some 55 nomenclatural changes have been made, for example, *Mickelopteris* Fraser-Jenk., gen. nov. in the family Pteridaceae, and these changes can be identified readily as they are listed in bold in the taxonomically arranged index of accepted and excluded taxa at the end of Part 1.

The authors are to be congratulated on a very welcome addition to current knowledge of the rich diversity of pteridophytes in Asia.

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